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POLYCHAETES

Vol. I

P. V. Ushakov

POLYCHAETES OF THE SUBORDER PHYLLODOCIFORMIA OF THE POLAR BASIN AND THE NORTHWESTERN PART OF THE PACIFIC

(FAMILIES *Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae, and Lacydoniidae*)

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(Mnogoshchetinkovye chervi)

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P. V. Ushakov

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3 *PREFACE*

Numerous new data on Polychaeta have been collected from different parts of the oceans of the world, and many families therefore require revision. This work is an attempt to summarize information on the Phyllodocidae, Alciopidae, Tomopteridae, Typhloscolecidae and Lacydoniidae from the northern seas of Europe, the Polar Basin and the Northwest Pacific, from the Bering Sea in the north to the Gulf of Tonkin in the south. Collections made by Russian marine expeditions, now in the Zoological Institute of the Academy of Sciences of the USSR (Leningrad), formed the basic material for this summary. Nearly 100 species and lower units of these families are described. The material collected on board the "Vityaz," mainly from the abyssal depths of the Pacific Ocean, contained 10 new species and one new genus, demonstrating the insufficient exploration of the open ocean. Descriptions of most species have been prepared from our material and illustrated by original drawings: only the diagnoses of a few species, not represented in our collections, have been taken from the literature. The systematic survey also includes some pelagic species from the Northeast Pacific, although they probably occur also in the western part of the ocean. Our material often made it necessary to revise the diagnoses of some genera. Keys to species and genera which do not occur in the Polar Basin and the North Pacific have sometimes been included for a more precise definition of the position of some units in the general classification of marine Polychaeta (these are marked with an asterisk in the keys). In the synonymy, reference is generally made to publications which give records of these species in the area studied.

The families dealt with in this work have varying numbers of species and differ markedly in their ecology. The family Phyllodocidae sensu lato is the largest, mainly benthic, and often forms large colonies in coastal zones. The status of the Lacydoniidae, a family which contains only a small number of benthic forms, has been accepted only recently; this family, which was formerly included in the Phyllodocidae, is an intermediate link between the Phyllodocidae and the Nephtyidae. The other families, the Alciopidae, Tomopteridae and Typhloscolecidae, contain only planktonic species, found
4 mainly in the open sea. The Alciopidae certainly have close genetic relations with the benthic Phyllodoçidae, but the other two families are very aberrant Polychaeta, which developed characteristic adaptations to pelagic life. The Tomopteridae are probably a very ancient, highly specialized group, and some Typhloscolecidae may be neotenic forms in connection with their transition to ectoparasitism. All the above families, despite their different biology and external morphology, have been placed in the suborder Phyllodociformia. This name was proposed by Levinsen (1882) without his defining its systematic rank (superfamily, suborder). This group is precisely defined in the present work. The suborder Phyllodociformia belongs to

the order Phyllodocemorpha (Livanov, 1940), which includes the marine polychaetes with the most primitive characters. Some species described in this work have been compared with related species from other regions, particularly with species received from A. Eliason (Naturhistoriska Museet, Göteborg) and M. Jones and M. Pettibone (Smithsonian Institution, Washington); we have also compared some species with the types of Prof. P. Fauvel, in the Muséum National d'Histoire Naturelle, Paris, where I was accorded great consideration by Prof. A. Chabaud. In the description of pelagic Polychaeta we were substantially helped by the plankton collections of the Soviet Antarctic Expedition on the "Ob"; these were identified by N. Tebble (British Museum, Nat. Hist.) and are at present deposited in the Zoological Institute of the Academy of Sciences of the USSR.

I wish to express my deep gratitude to all specialists, from the Soviet Union and other countries, who placed their material at our disposal. I am grateful to the staff of the Marine Research Laboratory of the Zoological Institute (USSR) for their cooperation during my long research on the marine fauna in their laboratory. Valuable assistance was given during the writing of this book by Profs. A. A. Strelkov and A.V. Ivanov. I am much indebted to V. A. Sveshnikov, who prepared descriptions and drawings of larval forms. Many of the illustrations were done by T. N. Shishlova.

*SYSTEMATIC INDEX OF SPECIES**

ORDER ***Phyllodocemorpha***

SUBORDER **Phyllodociformia**

I. Family **Phyllodocidae** Oersted, 1843

1. Subfamily Phyllodocinae Oerst 1843

1. Genus *Lugia* Quatrefages, 1865

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1. *L. abyssicola* Uschakov sp. nov. 116

2. Genus *Mystides* Théel, 1879

1. *M. borealis* Théel, 1879 120
2. *M. rarica* (Uschakov, 1958) 121
3. *M. schroderae* Uschakov sp. nov. 121
4. *M. southerni* Banse, 1954 122

3. Genus *otomystides* Czerniavsky, 1882

1. *P. levensteinae* Uschakov sp. nov. 124
2. *P. orientalis* Uschakov sp. nov. 125
3. *P. occidentalis* (Ditlevsen, 1917) 126

4. Genus *Genetyllis* Malmgren, 1865

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2. *G. castanea* (Marenzeller, 1879) 127

5. Genus *Phyllodoce* Savigny, 1818

Subgenus *Phyllodoce* Savigny, 1818, s. str.

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1б. *P. laminosa brevis* Zachs, 1933 131

2. *P. gracilis* Kinberg, 1866 131
3. *P. malmgreni* Gravier, 1900 132

Subgenus *Anaitides* Czerniavsky, 1882

4. *P. (Anaitides) groenlandica* Oersted, 1842 133
5. *P. (A.) maculata* (Linné, 1767) 134
6. *P. (A.) mucosa* Oersted, 1843 135
7. *P. (A.) citrina* Malmgren, 1865 136
8. *P. (A.) chinensis* Uschakov et Wu, 1959 137
9. *P. (A.) madeirensis* Langerhans, 1880 138
10. *P. (A.) papillosa* Uschakov et Wu, 1959 139

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* [This index has been photographically reproduced from the Russian original. The pages indicated are Russian page numbers which appear in the left-hand margin of this text.]

6. Genus *Paranaitis* Southern, 1914

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1. *P. wahlbergi* (Malmgren, 1865) 140
2. *P. polynoides* (Moore, 1906) 141
3. *P. caecum* Uschakov sp. nov. 142

7. Genus *Chaetoparia* Malmgren, 1867

1. *C. nilssoni* Malmgren, 1867 143

8. Genus *Eulalia* Savigny, 1817

1. *E. viridis* (Linné, 1767) 146
2. *E. bilineata* (Johnston, 1840) 148
3. *E. sigeformis* Annenkova, 1937 149
4. *E. austrophylloformis* Uschakov sp. nov. 150
5. *E. gravieri* Uschakov sp. nov. 150

9. Genus *Steggoa* Bergström, 1914

1. *S. pacifica* Imajima, 1964 152

10. Genus *Eumida* Malmgren, 1865

1. *E. sanguinea* (Oersted, 1843) 153
2. *E. albopicta* (Marenzeller, 1879) 154
3. *E. tubiformis* Moore, 1909 155
4. *E. minuta* (Ditlevsen, 1917) 156
5. *E. fusigera* (Malmgren, 1865) 156
6. *E. nigrimaculata* (Moore, 1909) 157

11. Genus *Pterocirrus* Claparède, 1868

1. *P. macroceros* (Grube, 1860) 160
2. *P. slastnikovi* Annenkova, 1946 161
3. *P. notoensis* (Imajima, 1967) 161
4. *P. imajimai* Uschakov sp. nov. 162

12. Genus *Austrophyllum* Bergström, 1914

1. *A. sphaerocephala* (Levenstein, 1961) 164

13. Genus *Vitiazia* Uschakov, 1953

1. *V. dogieli* Uschakov, 1953 165

14. Genus *Vitiaziphyllum* Uschakov gen. nov.

1. *V. nuchalum* Uschakov sp. nov. 167

15. Genus *Notophyllum* Oersted, 1843

1. *N. foliosum* (M. Sars, 1835) 169
2. *N. imbricatum* Moore, 1906 170

16. Genus *Nipponophyllum* Imajima et Hartman, 1964

1. *N. japonicum* (Marenzeller, 1879) 171
2. *N. sagamianum* (Izuka, 1912) 172

17. Genus *Eteone* Savigny, 1820

Subgenus *Eteone* Savigny, 1820, s. str.

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3. *E. delta* Wu et Chen, 1963 176

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4a. *E. spetsbergensis spetsbergensis* Malmgren, 1865 177
4б. *E. spetsbergensis bistriata* Uschakov, 1953 177
5. *E. vitiazi* Uschakov sp. nov. 178
6. *E. lactea* Claparède, 1868 179

Subgenus *Mysta* Malmgren, 1865

7. *E.* (Mysta) *barbata* Malmgren, 1865 179
8. *E.* (M.) *ornata* Grube, 1877 181
9. *E.* (M.) *maculata* (Treadwell, 1920) 182
10. *E.* (M.) *tchangsii* Uschakov et Wu, 1959 183

2. Subfamily Lopadorhynchinae Claparède, 1870

18. Genus *Lopadorhynchus* Grube, 1855

1. *L. appendiculatus* Southern, 1909 185
2. *L. brevis* Grube, 1855 186
3. *L. krohnii* (Claparède, 1870) 186
4. *L. uncinatus* Fauvel, 1915 187

19. Genus *Pelagobia* Greeff, 1879

1. *P. longicirrata* Greeff, 1879 188

20. Genus *Maupasia* Viguier, 1886

1. *M. coeca* Viguier, 1886 190
2. *M. brodskyi* Uschakov, 1957 190

21. Genus *Pedinosoma* Reibisch, 1895

1. *P. curtum* Reibisch, 1895 191

3. Subfamily Pontodorinae Bergström, 1914

22. Genus *Pontodora* Greeff, 1879

1. *P. pelagica* Greeff, 1879 192

4. Subfamily Iospilinae Bergström, 1914

23. Genus *halacrophorus* Greeff, 1879

1a. *Ph. pictus pictus* Greeff, 1879 194
1б. *Ph. pictus borealis* Reibisch, 1885 194

II. Family **Alciopidae** Ehlers, 1864

1. Genus *Torrea* Quatrefages, 1850

1. *T. candida* (Delle Chiaje, 1841) 199

2. Genus *Naiades* Delle Chiaje, 1830

1. *N. cantrainii* Delle Chiaje, 1830 200

3. Genus *Vanadis* Claparède, 1870

1. *V. formosa* Claparède, 1870 202
2. *V. longissima* (Levinsen, 1885) 203

4. Genus *Alciopa* Audouin et M.-Edw., 1833

1. *A. reynaudii* Audouin et M.-Edw., 1833 204

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5. Genus *Plotohelmis* Chamberlin, 1919

1. *P. tenuis* (Apstein, 1900) 205

6. Genus *Alciopina* Claparède et Panceri, 1867

1. *A. parasitica* Claparède et Panceri, 1867 206

7. Genus *Krohnia* Quatrefages, 1865

1. *K. lepidota* (Krohn, 1845) 207
2. *K. excellata* (Uschakov, 1955) 208

8. Genus *Rhynchonerella* Costa, 1864

1. *R. gracilis* Costa, 1862 210
2. *R. petersii* (Langerhans, 1880) 210
3. *R. angelini* (Kinberg, 1866) 211

9. Genus *Watelio* Støp-Bowitz, 1948

1. *W. gravieri* (Benham, 1929) 212

III. Family **Tomopteridae Grube, 1848**

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Subgenus *Tomopteris* Eschscholzt, 1825, s. str.

1. *T. septentrionalis* Quatrefages, 1865 216
2. *T. elegans* Chun, 1888 217

Subgenus *Johnstonella* Gosse, 1853

3. *T.* (*Johnstonella*) *pacifica* Izuka, 1914 218
4. *T.* (*J.*) *helgolandica* Greeff, 1879 219

IV. Family **Typhloscolecidae Uljanin, 1878**

1. Genus *Typhloscolex* Busch, 1851

1. *T. muelleri* Busch, 1851 221

2. Genus *Travisiopsis* Levinsen, 1885

1. *T. lobifera* Levinsen, 1885 223
2. *T. levinseni* Southern, 1910 223
3. *T. lanceolata* Southern, 1910 224

3. Genus *Sagitella* N. Wagner, 1872

1. *S. kowalewskii* N. Wagner, 1872 225

V. Family **Lacydoniidae Bergström, 1914**

1. Genus *Lacydonia* Marion et Bobretzky, 1875

1. *L. papillata* Uschakov, 1958 227

2. Genus *Paralacydonia* Fauvel, 1913

1. *P. paradoxa* Fauvel, 1913 228

9 *INTRODUCTION*

GENERAL INFORMATION

The highly diversified appearance of marine Annelida explains the admiration of many investigators. The beauty of the Polychaeta, which are doubtless the most attractive of the invertebrates, can scarcely be conveyed in the dry language of the taxonomist, hence the following quotations from Hartwig's book "Das Leben des Meeres," which, though written over a century ago, describes vividly and fairly accurately some of the characteristics of polychaetes. After the opening observation, "the word worm is generally associated with the concept of imperfection; a worm is considered an uninteresting, repulsive creature...", Hartwig continues: "What surprising wealth of organs! What splendid formation! Truly, any complaint of scantiness or insufficiency is out of place. In external appearance marine Annelida are among the most magnificent creatures in the entire animal kingdom. You find in them the iridescence of the humming-bird, the metallic luster of the most beautiful beetles. The free-living genera, crawling like serpents through cracks in rocks, circling around, diving at the bottom of the sea, in sand, in mud, are especially beautiful. Admiring naturalists bestowed on them the names of pagan deities: Nereis, Euphrosyne, Alcione, Aphrodite." Hartwig quotes the words of Quatrefages, the great French specialist on polychaetes in the early 19th century: "Do not call violet the symbol of modesty, better have a look at our Annelida. What do they lack in splendor! Undoubtedly we still do not know many of them, some are just beginning to reveal their secret marvels, others hide under seaweed-covered rocks or in the sand and silt at the bottom of the sea..." These admiring words also apply to the species described here, albeit without such lively enthusiasm. In more modern scientific language, it may be stated without exaggeration that none of the marine invertebrates have the ecological plasticity and the wealth and diversity of morphological structures found in the Polychaeta.

In the general economy of the sea, the role of Polychaeta is tremendous. They represent a very important link in all processes of the production of living matter, and in particular, they are the basic food, rich in calories, of numerous
10 fishes. One gram of dry substance of Nereis diversicolor contains over 5500 calories (Vinogradov, 1948). Some polychaetes are eaten by man. It is well known that the palolo of the Pacific Ocean (Eunice viridis) is a commercial item during its mass reproduction near the coasts of Fiji and Samoa, when practically the entire population engages in collecting the worms. The Japanese palolo, Tylorhynchus chinensis (Nguyên-Công-Tiêu, 1931), is used as food in Japan and Vietnam. Numerous polychaetes are collected for use as bait in fishing (Okuda, 1933). There are also species which cause damage. The Nereidae, for example, invade paddy fields and destroy the roots of rice (Kaburaki, 1926). Damage is

occasionally caused by the Serpulidae, which foul the bottom of ships and underwater constructions, and also damage *Laminaria* (blade-kelp) and other edible seaweed. Poisonous species also exist (Halstead, 1965).

There are numerous publications on the morphology and systematics of Polychaeta and, recently, on their development and reproduction. Polychaeta are the subject of detailed ecological and physiological research, and attempts have even been made to "train" them; the attention of scientists has been drawn to some problems of neurosecretion, connected with the phenomenon of epitoky; of special interest is the nervous system of polychaetes, which in some cases has served as the principal scheme for cybernetic calculations. Problems of phylogeny, of the construction of a natural classification of the Polychaeta, have also been studied, but these are still in their initial stages.

Over 200 scientists are at present studying polychaetes in various countries (see Newsletter on Polychaete Research, University of Maine, Marine Laboratory, Vol. 1, 1968; Vol. 2, 1969). The number of species of Polychaeta described was 10,812 in 1958 (5341 accepted), and the number of genera 1366 (720 accepted); 100 new genera and about 1000 new species have been described in recent years (Hartman, 1959, 1965a). There are about 70 families. These figures do not, of course, exhaust the diversity of the fauna. Numerous interesting small polychaetes have been discovered recently, and their number will grow as the study of the littoral interstitial fauna progresses. The largest and most unexpected additions will probably be found by a detailed study of the abyssal fauna, in which improved methods of collection will be used.

HISTORICAL REVIEW

Linnaeus recorded in the "Systema naturae" (1767, 12th edition) *Nereis maculata* and *N. viridis*, which are at present considered as the types of two important genera of Phyllodocidae, *Phyllodoce* Savigny and *Eulalia* Savigny. Fabricius (1780) described in the "Fauna Groenlandica" *Nereis flava*, which became the type of the third genus *Eteone* Savigny of the family Phyllodocidae.

The Phyllodocidae were first established as a distinct group by Oersted
11 (1843, p. 25), who united the genera of Phyllodocidae known at that time, *Phyllodoce*, *Eulalia*, *Eteone* and *Notophyllum*, into a "divisio Phyllodoceae," which he placed in the family Nereidae. This family had at the time a very wide composition and included the Alciopidae, Syllidae, Hesionidae, Glyceridae, Nephthyidae and others. The first detailed classification of polychaetes was given by Grube (1850).* He established the family Phyllodocea, including in it, however, the genera included at present in the families Hesionidae and Alciopidae. These families were separated from the Phyllodocidae by Ehlers (1864) and Malmgren (1865, 1867). The family Tomopteridae was established by Grube for the special group Gymnocopa in contradistinction to the Chaetopoda, which included all other families of polychaetes. The family Typhloscolecidae was established by Uljanin (1878).

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* The work of Quatrefages (1865) contains a brief historical review of the different classifications of Annelida, from Cuvier and Lamarck onward.

The literature on the families of polychaetes dealt with in this work is very large, and it is not possible to give a comprehensive historical review. However, the work of Gravier (1896) on the family Phyllodocidae deserves special mention. It is out of date in some respects, but it clarified in detail the comparative-anatomical characteristics of this family. Bergström (1914) published a monograph on the Phyllodocidae, with a very detailed classification of genera which is not correct in all respects; there are unfortunately some systematic mistakes. Recent studies, mainly systematic, which contain numerous data on the Phyllodocidae of the Atlantic and Pacific coasts of North America, are the works by Berkeley and Berkeley (1942—1964), Hartman (1936—1968) and Pettibone (1963). The Polychaeta of the region around Japan are dealt with in detail in the monograph of Imajima and Hartman (1964).

Pelagic Polychaeta are discussed in some special publications. The studies of Fauvel (1916), Wesenberg-Lund (1935, 1939), Stop-Bowitz (1948), Dales (1955a, 1957) and Tebble (1962) are of great importance for the systematics of pelagic Polychaeta.

RECENT WORK ON THE SYSTEMATICS OF THE PHYLLODOCIDAE

The wide activity of expeditions and the abundant material collected by them make it necessary to find reliable external characters which permit rapid identification of species and smaller taxonomic units. The large number of new species described in recent years has considerably complicated many problems of systematics, and the simple classification of some families is no longer satisfactory in the light of our present knowledge. The concepts taxonomy and systematics are not entirely synonymous: taxonomy
12 is restricted to the description of the important characters (diagnostics), while systematics deals with the construction of a natural system, i. e., an attempt to clarify phylogenetic relationships. This requires comparative-anatomical studies, which are very few until now. In particular, during the construction of a natural system of the Phyllodocidae the structure of the nervous system of the anterior segments is of great importance, as was already pointed out by Pruvot (1883). Recent systematists usually have to be satisfied using only external morphological characters, although they are unreliable in many cases.

The Phyllodocidae, especially the benthic species, are one of the most difficult groups. They show little diversity in morphological characters and have a uniform, relatively simple pattern of structure, which makes determination difficult, particularly of fixed material.

The important morphological characters of the Phyllodocidae are the following: the form of the cephalic lobe and of the cephalic tentacles, the character of the peristomal segments (their more or less distinct separation from each other and from the cephalic lobe), the number and situation of the peristomal cirri, the structure of the proboscis, and the form of the parapodia with dorsal and ventral cirri, setae and anal cirri. The coloration of the body and appendages is important for identification but it disappears after fixation. Many of the above characters are very variable, and the form of the soft appendages often depends on the method of fixation.

Description of a species requires live material, but this is rarely available. Unfortunately, our study had to be carried out mainly on material preserved in alcohol, and some specimens were damaged, and not all appendages were preserved. Only at the Murmansk biological stations in the Kola Gulf and at Dal'nie Zelentsy, in the Sea of Japan and the Yellow Sea, and on Hainan Island was live material available, so that ecology and biology could be studied.*

13 Descriptions are often very short and do not permit identification. It is possible that different subspecies were sometimes described under the same name. A very wide geographical distribution has therefore been attributed to many species, which further study may not confirm. A study of populations of widely distributed species, carried out on large numbers from the periphery of their distribution range, should be of great interest. Such a study should be made of some common species, e.g. Eulalia viridis and Eumida sanguinea, recorded from widely different regions of the oceans. There are few data on the intraspecific variation of Polychaeta.

According to the Catalogue of the Polychaetous Annelids of the World, by Hartman (1959, 1965), the family Phyllodocidae contains 29 genera and about 250 species, the Alciopidae 10 genera and 42 species, the Lopadorhynchidae 6 genera and 20 species, the Lacydoniidae 3 genera and 6 species, the Jospilidae 4 genera and 7 species, the Pontodoridae 1 genus and 1 species, the Typhloscolecidae 3 genera and 14 species and the Tomopteridae 2 genera and 40 species. A slightly different classification has been used in this work and the Lopadorhynchidae, Iospilidae and Pontodoridae are considered as subfamilies of the Phyllodocidae sensu lato (see the section on phylogenetic relationships in the Phyllodocidae, p. 63).

MORPHOLOGICAL-FUNCTIONAL SURVEY

Size and form of the body

The family Phyllodocidae contains very small forms, e.g. the pelagic Pedinosoma curtum and numerous species of the interstitial fauna, Hesionura (= Eteonides) fragilis and others, which are only 1 or 2 mm long. On the other hand, there are also giants, e.g. Phyllodoce laminosa, which is over 750 mm long. The average length of most benthic Phyllodocidae is about 50–100 mm. The Alciopidae includes species 20–30 mm long (Plotohelmis tenuis) and some larger species over 300 mm long (Vanadis formosa). Good specimens of Alcionidae are rarely found in the plankton. The largest specimen of Tomopteris recorded was 135 mm long (Tebble, 1962, p. 386), but the normal length is

---

* For maintenance of worms in captivity, in addition to the usual nurse-ponds, the small portable aquarium with aeration proposed by Reish (1966) can be recommended. For anesthesia, magnesium sulfate or magnesium chloride is added to seawater to a 4–8% solution, in which the worms are kept for 10 minutes to an hour (according to size). The intestine is emptied rapidly and the pharynx is everted; if this does not take place, gentle pressure is applied to the anterior part of the body. Anesthesia can also be obtained in 10 parts seawater with 1 part alcohol. For preservation of the natural coloration, Bellan (1964) suggested fixation in a mixture of 45 parts seawater, 40 parts fresh water and 15 parts of 40% formalin, after neutralizing the solution with calcium carbonate, so that the pH is 7. The worms retain their coloration and remain soft for more than 15 years.

20–40 mm. All Typhloscolecidae are relatively small, not over 30 mm long, and Typhloscolex muelleri is usually less than 5 or 7 mm long. The rare Lacydoniidae are never large, not more than 40 mm long.

There are species of different size also in other families. Thus, in the Eunicidae sensu lato there is the small Ophryotrocha (less than 10 mm long) and Eunice gigantea which may be 1–3 m long. In the Aphroditidae sensu lato, some species of Polyodontes are very large (to one meter). This is also the case in some highly specialized families, e.g. the Sabellidae and Serpulidae.

The largest Phyllodocidae also have the greatest number of segments (Phyllodoce laminosa has to 800 segments); the same is the case in the Eunicidae. However, this does not apply to all Polychaeta. The size
14 of Aphroditidae sensu lato does not depend on the number of segments: e.g. Eulagisca gigantea is over 150 mm long and Harmothoe imbricata less than 50 mm, but the number of segments is the same, 37–38; Laetmatonice producta has 42–50 segments, and is 135 mm long, and Pholoe minuta, with 70 segments, is only 20 mm long.

The length of Phyllodocidae depends on the state of the muscular-cutaneous sac. During movement, they become considerably larger and narrower and then shorter and thicker. The function of maintaining the form of the body is carried out mainly by the coelomic fluid, and not by the integument; the coelomic fluid in species with weak intersegmental septa may move from one part of the body to another, because of the contraction of muscles.

Benthic Phyllodocidae have an elongate body, slightly wider anteriorly and gradually narrowing to a pointed posterior end; the body is distinctly flattened dorsoventrally, the dorsal side more convex than the ventral. A longitudinal media groove is sometimes present on the ventral side, which facilitates crawling on the bottom. This "wormlike" form of body is also characteristic for species of numerous other families with a free, active mode of life. However, polychaetes with a short and broad, oval or ovoid body also occur (some Amphinomidae), and these change little their form when crawling. A constant form of body is observed in numerous Aphroditidae, which has to be considered as a progressive phenomenon.

The great diversity of form of many tubicolous worms is due to the peculiar conditions of their existence in fixed "portable" tubes. Different parts of the body, with specific functions, often differ markedly in their morphology, e.g. in the Chaetopteridae, Sabellariidae, Pectinariidae and other families (p. 17). The form of the body of benthic Phyllodocidae is very simple, corresponding to their primitive structure, which is expressed in their external morphology (homonomy of segments, simplified protective cephalic armature, simple parapodia, etc.), in their internal organization (protonephridia, absence of a branched vascular system, subepithelial situation of the ventral nerve cord) and in the primitive character of ontogenesis and of the types of larvae.

Coloration and its protective importance

Polychaetes sometimes have a variegated coloration with a complicated pattern which is difficult to describe; parts of the body are often of different color. The integument of most polychaetes is strongly iridescent, with a metallic sheen of all colors of the spectrum, which is due to the microstructure of the cuticular layer. Coloration is often related to the presence of pigments in the integument, particularly phyllodocin, which causes the green coloration of Eulalia viridis. The viscera are often visible through the thin cuticle, the intestine, sexual products, blood. Some variation is sometimes due to the maturity of the sexual products, and the coloration may differ in mature males and females. Thus, mature females of Eteone longa are dark green or brown, and males light yellowish. This is partly due to sexual dimorphism which, however, is never so marked in the Phyllodocidae as in the Syllidae, Spionidae or other families.

The diversity of coloration is sometimes reflected in the names: Eulalia viridis is predominantly bright green, Eumida sanguinea reddish, Phyllodoce maculata has a gray checkerboard pattern, Eteone (Mysta) picta has a pattern with numerous transverse spots on each segment, E. lactea is milky white or beige, etc. Some Phyllodocidae are bright orange, others vermilion, but the dorsal cirri are usually of a different color (darker or lighter) than the dorsal surface of the body. The color pattern of the Phyllodocidae is usually the same on the whole body. The coloration of the body and appendages is important systematically, but the colors fade rapidly in alcohol. Phyllodocidae which live in the benthic vegetation have the brightest coloration, while abyssal species and forms which burrow into the bottom are usually uniformly light beige or yellow.

The variegated, bright "crown of tentacles" of the Sabellidae may repel enemies (defensive function?), but in most cases, coloration is cryptic. In particular, the predominantly greenish and dark brown coloration of the Phyllodocidae gives excellent camouflage in the aquatic vegetation; the transparency of pelagic polychaetes makes them invisible in water; many Alcionidae are recognizable only by their dark telescopic eyes, and Tomopteridae by the small dark orange rosette-like organs on their fins.

Camouflage may be attained also by more complicated methods. The elytra of some Aphroditidae have in addition to their variegated coloration a complicated sculpture, on which small hydroids and Bryozoa occasionally settle, so that the worms become invisible on the background. In forms which burrow in the sand (Psammolyce, Brada, Stylariodes and others), the integument may become so densely covered with particles of sand, glued on by the secretion of cutaneous glands, that the animals can be found only with great difficulty. There is sometimes real mimicry. This is observed in the commensals of sponges (Euphrosyne and Spinther). Sponges are not only protected by skeletal spicules, they are stated also to discharge poisonous substances into the water. Travisia forbesii and Aricia foetida, which burrow into the ground, have a strong offensive smell of sulfuretted hydrogen. However, the Phyllodocidae rely for protection only on their cryptic coloration.

Bioluminescence

Bioluminescence, emission of bright violet, pale blue or greenish light, has been observed in many polychaetes, errant and sedentary: Alciopidae, Tomopteridae, Aphroditidae, Syllidae, Chaetopteridae, Cirratilidae and Terebellidae. In the Alciopidae, bioluminescence has been observed in

16 Corynocephalus and Calizonella (= Krohnia), but it is probably present also in other species of this family. In the Tomopteridae luminescence is emitted by rosette-like organs, situated on the parapodia. These organs consist of yellow photogenic cells surrounded by a layer of high transparent cells, and below them is a ganglion with processes into the transparent cells (luminescence is apparently intracellular). Pontodora pelagica and other small pelagic species are probably also bioluminescent. In the errant species, bioluminescence has been studied in detail in the Aphroditidae (Bonhomme, 1942; Nicol, 1953, 1954; Koshtoyants, 1957).

The biological function of bioluminescence is attraction between males and females, which is of great importance for pelagic forms as they do not form dense populations. In many species of Syllidae, the phenomenon is observed only during the period of epitoky — "swarming," or "epigamic dances."

In benthic polychaetes, luminescence is sometimes a defensive reaction: in some cases its effect is only to frighten the enemy, but in others the phenomenon is more complex. Thus, if a specimen of Polynoidae is attacked, the posterior elytra instantly "light up" and are discarded (an example of autotomy); the discarded elytra continue to emit light for some time, and the worm meanwhile slips away.

Integument, mucilaginous cases and tubes

Polychaeta have a soft integument, which has no skeletal function; they therefore never molt, like arthropods and some nematodes, the integument of which forms a skeleton. The elasticity of the body is due to the turgor of the coelomic fluid isolated from the external environment ("hydraulic skeleton").

The skin of Polychaeta consists of a simple epithelium, covered by an elastic cuticle and lined on the inside with a basal membrane of homogeneous structure. The cuticular layer consists of fine fibrillae crossing at right angles, which produce the characteristic metallic (iridescent) sheen of the integument.

Ciliated epithelium, characteristic for the more primitive parenchymatous worms (Platyhelminthes, Nemertini), is strictly localized in the Polychaeta, mainly on the cephalic and podial processes, branchiae, etc., and at the base of the sensory pits and fossillae (nuchal organs). Ciliated epithelium is relatively extensive in the Phyllodocidae and serves for the constant washing of the cutaneous covering, through which respiration takes place. Areas of ciliated epithelium in the Phyllodocidae are situated on the podial processes which are surrounded by characteristic stripes of this epithelium. These areas are especially extensive on the dorsal cirri; in species of Phyllodoce, areas of ciliated epithelium are concentrated on the posterior side of the cirri, near its lower margin, and form wide convex ridges (tori) with membranes consisting of glued-together cilia. Ciliated epithelium is present in the Phyllodocidae also on the dorsal side of the segments, in the form of hoops usually coincident with the secondary annulation.
17 Such transverse "belts" on the dorsal side of the segments are present also in some small Syllidae, and in the Eunicidae in Ophryotrocha puerilis, which is considered as a neotenic form. Similar ciliated areas have

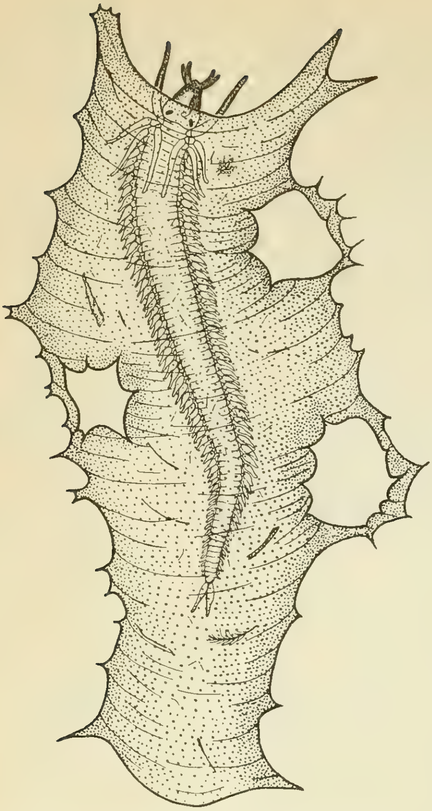

FIGURE 1. Mucous case of adult Eulalia viridis (after Buzhinskaya and Lebskii, 1971)

been observed in most species of Archiannelida, Protodrilus, Nerilla and others. Larvae of polychaetes often have a continuous ciliated covering of epithelium. The retention of ciliated epithelium in many parts of the integument of adult Phyllodocidae is evidence of their primitive nature.

Between the supporting epithelial cells, which are of elongate prismatic or cubical form, there are numerous sensory cells and numerous gland cells which secrete mucus through small pores in the cuticle. In the Phyllodocidae, these mucus-secreting cells are distributed uniformly in the epidermis. Rarely 2 or 3 are grouped together; they may be present in dense groups near the excretory pores around the base of the parapodia, not unlike in glandular organs.

Abundant secretion of mucus is characteristic for nearly all the Phyllodocidae. Mucus facilitates movement on the bottom and particularly in the bottom, due to its cementing properties which strengthen the inner side of the temporary passage burrowed in the ground. The Phyllodocidae, which do not build permanent tubes, use the mucus for the construction of temporary "cases" (Figure 1) which protect the integument, through which respiration takes place, from being clogged with detritus and particles of silt. For irrigation of these cases, which have lateral windowlike openings, the Phyllodocidae and other tubicolous polychaetes make twisting dorsoventral movements of the body, inducing a constant flow of new water into their shelters.

18 Temporary mucous cases may be considered as the prototype of permanent tubes. The mucus secreted by polychaetes, which build tubes that have to last a long time, hardens rapidly and layers of strong "parchment" are formed. Their structure resembles that of the cuticle of the worms. Some polychaetes add particles of the soil to the mucus, and may also use fragments of mollusc shells, Foraminifera, spines of sea urchins, spicules of sponges, shreds of seaweed, etc. Many polychaetes carefully select suitable material: thus, Onuphis conchylega uses for its tubes mainly crushed shells of mussels. The quiver-shaped tubes of Pectinaria, which have the form of an elephant's tusk, are formed by a single layer of sand grains solidly glued together, resembling a mosaic. The long thin tubes of the small Myriochele (Oweniidae) consist mainly of transparent spicules of sponges, between which are inserted, at intervals, oblong black mineral particles, so that the whole structure appears striped. Like Pectinaria, Hyalinoecia tubicola (Eunicidae) carries its transparent

chitinous case which resembles a goose quill. The tubes of many polychaetes are straight and of uniform width, or they become narrower toward both ends; the tubes are often sinuous and of irregular form. They are usually dug deep into the ground, with only their ends showing on the surface. Large colonies of entangled tubes are often found attached to the substrate. The tubes of Serpulidae are impregnated with lime, which distinguishes them from the tubes of all other species; they are milk white or pink, rarely semitransparent. Characteristic for many species is a sculpture consisting of numerous transverse folds, longitudinal ridges and undulant keels. The tubes of Serpulidae are attached to rocks, shells of molluscs and crabs, the thallus of seaweed, etc.; only Ditrupa (Serpulidae), named "sharp awl" by French fishermen, lives free in silt (it is sometimes mistaken for Dentalium). The structure of the tubes and their form are often so specific that they could be used as systematic characters, so that the species can be determined by its tube. The complicated process of construction of the tube has been described in detail for many species (Ziegelmeier, 1952; Hedley, 1958; and others). The very characteristic method of tube construction of Panthalis (Polyodontidae), which has special large "gossamer-glands," uses the long, elastic, golden threads secreted by the glands as the basis for the tubes; the "gossamer-glands," which have the form of very large, curled flagella, are situated in the parapodia (Watson, 1895).

Tubes are constructed not only in sedentary families but also in many errant polychaetes. As indicated by the great diversity of types of tubes, 19 the ability to build tubes apparently developed independently in different families. The Phyllodocidae, however, do not build tubes. Some of them (Eteone) make deep passages in silty-sandy ground, the walls of which differ from the surrounding ground in color and consistency. Phyllodocidae often use natural hollows in the ground, or hide among seaweed. Only some abyssal species (Notophyllum (= Austrophyllum) caecum, ?Lugia abyssicola) have been found in tubes, but these were probably not their own tubes, but those of other polychaetes, into which they entered accidentally.

External segmentation

The body of all polychaetes is segmented, but the segmentation may differ markedly, not only morphologically, but also in origin. As regards the method of formation, larval and postlarval segments have to be distinguished (Ivanov, 1944). Larval segments are formed simultaneously during the metamorphosis of the larva; postlarval segments are formed gradually, as the worm grows from the prepygidial zone of growth.

The number of larval segments of polychaetes, compared with arthropods, in which this number is constant (2 to 4 segments), is large, and varies in the different families. Thus, the larvae of Polynoidae have 7 segments, those of the Sigalionidae 5 and those of the Nereidae and Syllidae 3—4 segments. The larvae of some sedentary polychaetes have to 13 segments (Spionidae, Chaetopteridae). The larvae of the Phyllodocidae have 7, those of the Tomopteridae 5 segments (see "Reproduction and development"). With the larval and postlarval segments is connected the primary heteronomy, which later often affects the anatomy of the metameres (larval segments normally do not form sex glands), but this does not always determine the final external heteronomy of segments. The external heteronomy of the segments, as will be shown later, is mainly of an adaptive character, according to the specific habitation and mode of life.

The larvae of Phyllodocidae have 7 segments, but only the 2–3 anterior, the peristomal segments, differ in their morphology from the other segments, which are of homonomous appearance. There is no morphological difference between the larval and postlarval segments in the Phyllodocidae. However, in the Nereidae, the difference between the larval and postlarval segments becomes more marked during postlarval development: all four larval segments, 3 of them with setae, become fused into the large peristomium (Sveshnikov, 1960).

The number of segments of the body varies considerably. In some species, the number of segments increases during growth and may become very large (several hundred); in other species, the number of segments is limited. In species with an indefinite number of segments, the formation of new segments from the prepygidial zone of growth does not cease with the beginning of maturity. A large number of segments is a primitive character, but it is not restricted to the Phyllodocidae, and occurs also in other families, particularly in the Eunicidae, Terebellidae, Sabellidae and Serpulidae. Only in the narrowly specialized family Pectinariidae do all species have practically the same number of segments (about 30).

Among the benthic Phyllodocidae are species with a relatively small number of segments, a few dozen (Mystides, Protomystides), and species with several hundred segments (e.g. Phyllodoce laminosa, with over 800 segments). Most Alcionidae have a large number of segments, but this number is constant in numerous pelagic polychaetes and is used as a specific character (Lopadorhynchus, Tomopteris).

In addition to the primary annulation, which corresponds to the internal metamerism (see below), secondary annulation is often present (pseudosegmentation) which is not connected with the true segmentation of the body. Secondary annulation usually consists of incomplete grooves, mainly on the dorsal side of the segments. There are usually 2 or 3 such grooves on each segment, but there may be more. Secondary annulation, which is present in species of widely different families, may be considered as pseudometamerism, or as metamerism of a lower order. Secondary annulation in the Phyllodocidae is often associated with the presence of ciliary belts and different pigmentation on the dorsal side.

If all the segments of the body have a more or less uniform structure, the segmentation is termed homonomous. However, the segments often have a different morphology in different parts of the body, and this segmentation is termed heteronomous. Homonomy should be considered as the simplest, and therefore primitive, type of the segmentation of polychaetes. If segmentation is homonomous, all podial appendages have the same function, mainly locomotory and respiratory. Such a homonomy of segments is present in some errant families, but an absolute homonomy of all segments does not occur in errant families either: the anterior, peristomal segments, which take part in finding food, differ markedly from the other segments of the body in that their cirriform appendages are more elongate, and the posterior segments are usually underdeveloped.

The most complete, classical homonomy of segments is present in the benthic Phyllodocidae. Pelagic forms show further differentiation of the segments. Most species of Hesionidae, Syllidae and Nereidae have more or less the same homonomous structure of segments as the Phyllodocidae, but this homonomy is interrupted during the period of epitoky in the Nereidae.

The beginning stage of formation of secondary heteronomy, connected with division of function between different segments, is present in the Aphroditidae sensu lato: some of their segments bear scales (elytra), others cirriform appendages. This is so because in addition to the functions of movement, some segments have also the function to prevent clogging of the integument, while other segments have a tactile and respiratory function. In all Aphroditidae a strict alternation of scales and cirri from one segment to the other is present on the 5th to the 23rd segment. Such an alternation of segments
21 with scales and cirri has been named by Bekelemishev (1964) "metamerism of the second order." Behind the 23rd segment, scales are usually present on every third segment, and in species with a long body this alternation also disappears (particularly in commensals, e.g. in Arctonoe vittata, and especially in Polyeunoa laevis). Thus, if there is at all a metamerism of the second order, it is restricted to the anterior part of the body.

Heteronomy in the Nephtyidae consists mainly in the appearance on some segments of branchial semicoelomic processes, but the degree of their development is not the same on all segments. The process of interruption of the homonomy of segments goes even further in the family Glyceridae sensu lato: in Goniada and Glycinde the 40 to 70 anterior segments are uniramous, the others are biramous, and the whole body is divided into two distinctly different parts. In the family Eunicidae sensu lato, there are all transitions from an almost complete homonomy of segments (free-fossorial forms, e.g. Lumbriconereis) to a marked heteronomy (e.g. in Onuphis, Marphysa and others, which live in tubes). There is, thus, in many errant families a distinct tendency to heteronomy, which ensures better functioning of the parapodial complex. Only the benthic Phyllodocidae retain more or less the original homonomy, which proves their general primitiveness.

Heteronomy is most striking in sedentary tubicolous species, and the anterior isolated part of the body is therefore often named thorax, and the posterior part abdomen. An extreme form of differentiation and specialization of segments is present in species of Chaetopteridae and Sabellaridae, which is connected with their life in complicatedly constructed tubes which they cannot leave. There is no parallelism of morphological structure of certain parts of the body, a uniform plan of development of external heteronomy. Heteronomy developed in different ways in the different families, determined by the specific conditions and mode of life of each group of worms. However, heteronomy indicates a higher level of development. Differentiation of segments, caused by the increasing variety of functions, results in further diversity of structures, and thus in complication of the external morphology.

Division of the body into parts

The body of marine polychaetes can be divided into three main parts: 1) cephalic part, 2) body, and 3) caudal part.

The cephalic part consists of the cephalic lobe, or prostomium, and several modified anterior circumoral (peristomal) segments, which become fused in some errant polychaetes and form the distinctly differentiated

peristomium. The cephalic lobe develops from the upper hemisphere (episphere) of the trochophore, and it thus develops independently from all other segments. The mouth is always situated on the ventral side of the first segment, on the border with the cephalic lobe. The cephalic part bears various
23 tactile and distance-sensing organs (p.24). The main types of cephalic part in the Phyllodocidae are shown in Figure 2.

(22)

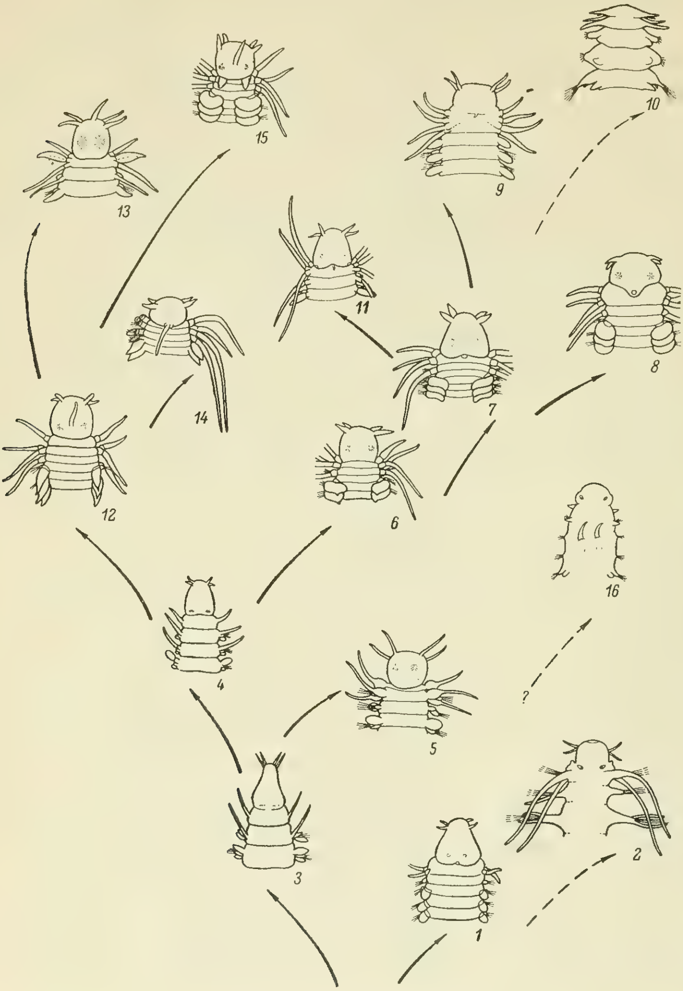

FIGURE 2. Principal types of cephalic part in the Phyllodocidae:

1) Eteone; 2) Pelagobia; 3) Lugia; 4) Protomystides; 5) Mystides; 6) Genetyllis; 7) Phyllodoce; 8) Paranaitis; 9) Chaetoparia; 10) Lopadorhynchus; 11) Zverlinum; 12) Eulalia sensu stricto; 13) Pterocirrus; 14) Austrophyllum; 15) Notophyllum; 16) Phalacrophorus.

The body consists of segments formed by the zone of growth immediately before the pygidium (anal lobe). All body segments are usually named metastomium.* The body segments bear a complicated podial complex, described separately (p. 27).

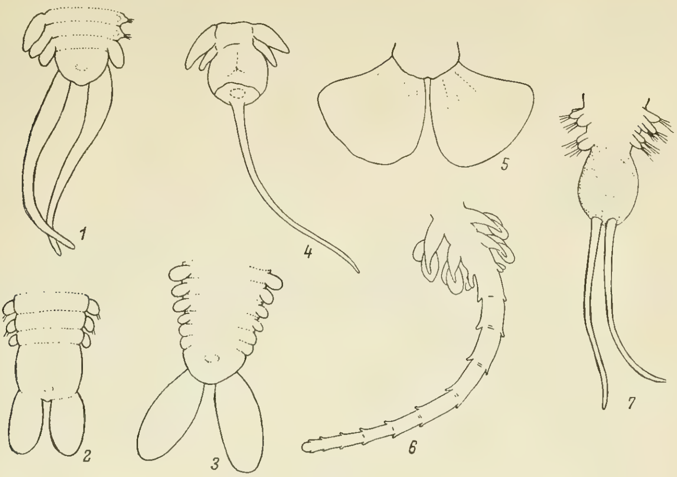

FIGURE 3. Posterior end of the body and anal cirri:

1) Austrophyllum sphaerocephala; 2) Eteone longa; 3) Eulalia bilineata; 4) Alciopa reynaudii; 5) Sagitella kowalewskii; 6) Tomopteris helgolandica; 7) Paralacydonia paradoxa.

The caudal part (Figure 3) consists of the anal lobe, or pygidium, which develops during the metamorphosis of the larva from the lower part (hyposphere) of the trochophore. The anus is usually situated at the end of the anal lobe or slightly displaced to the dorsal side; it has an unusual position only in Notopygos (Amphinomidae), in which it opens on the dorsal side of the body, 20–25 segments before the anal lobe (Ushakov and Wu Pao-ling, 1962). The position of the anus is normal in the Phyllodiciformes. The anal lobe is without setae; it may bear only the anal cirri, or urites. Benthic Phyllodocidae always have 2 anal cirri, which are elongate, spindle-shaped or rounded. The pygidium of the pelagic genus Phalacrophorus bears no anal cirri, but has instead a corolla of large cilia. The Typhloscolecidae have two very large, leaf-shaped anal cirri on the posterior end, resembling
24 the caudal fin Chaetognatha. The Alcionidae have 2 anal cirri, or only one (Figure 3, *4*). The caudal region also contains markedly modified, specialized posterior segments, usually in sedentary, tubulicolous forms. Thus, Pectinaria has at the posterior end a distinctly isolated, wide appendage formed by 5 or 6 segments, the so-called scapha, which has the form of a spoonlike plate. Still more peculiar is the specialized posterior end of the Sabellaridae, which live in cemented tubes and occasionally form veritable reefs in coastal zones (Dollfus, 1960). The caudal end resembles a long sausagelike tube which is curved posteriorly, toward the opening of the tube,

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* Some German authors, and also Livanov (1940), Beklemishev (1964), Ivanov (1958) and others, restrict the term metastomium to the first segment, immediately behind the cephalic lobe. This first segment should be properly named buccal, which describes its position also in the Phyllodocidae.

and almost as long as the body. Excrements are discharged directly into the water, without clogging the tube. The Phyllodocidae have no specialized caudal part, but several posterior segments are sometimes underdeveloped. A long "caudal appendage" formed by the underdeveloped segments is present in some species of Tomopteris (Figure 3, 6). A specimen of Eulalia viridis has been described with two caudal ends, a malformation caused by injury and regeneration (Wilson, 1937).

Cephalic part of the body and sense organs

The cephalic part, which consists of the cephalic lobe and several anterior circumoral segments, is markedly modified in different families, and there is no general uniform plan of structure of the cephalic end in all polychaetes. Particularly complicated are the structures connected with the tubiculous mode of life; it is difficult to find analogies or homologies between the various structures. The cephalic lobe is distinctly separated mainly in errant worms; it is markedly reduced in most sedentary polychaetes.

The cephalic lobe of benthic Phyllodocidae is usually elongate and slightly pointed; it is much larger than the following segments. There are two pairs of small frontal tentacles at the anterior end, one pair slightly displaced to the dorsal side, the other situated ventrally. There is also a single (median) tentacle on the dorsal side of the cephalic lobe of some species, usually slightly nearer to the posterior margin; the single tentacle is usually situated at the level of the eye. Nerve fibers from the middle of the brain enter these cephalic tentacles, which consist mainly of epithelial cells. The cephalic tentacles are tactile and chemical sense organs (mechano- and chemoreceptors).

The number of cephalic tentacles is fairly constant in most errant families. Thus, 2 cephalic tentacles are characteristic for the Nereidae, 2 or 3 for the Hesionidae, 3 for the Syllidae and Aphroditidae, and 4 for the Glyceridae and Nephtyidae. However, their number varies considerably in the Eunicidae: Lumbriconereis has no cephalic appendages, but this is a secondary phenomenon caused by its fossorial habit. Eunicidae which live in tubes (Onuphis and others) have 5 or 7 cephalic tentacles, some of
25 them very long, which enables them to palpate the surface of the ground for a considerable distance without leaving the tubes. In numerous errant polychaetes the cephalic tentacles are situated on "pedestals" — ceratophores, giving considerable mobility; the cephalic tentacles of the Phyllodicidae have no ceratophores. The Phyllodocidae are further characterized by the absence of palps, which are present in most errant polychaetes. In distinction to the cephalic tentacles, the coelomic cavity enters into the palps, which are always situated near the mouth. The palps are possibly more effective chemoreceptors than the cephalic tentacles.

Various nuchal organs are connected with the cephalic lobe. They have the form of invaginated papillae or fossae or grooves lined with ciliated epithelium. These organs are probably olfactory. In Phyllodoce, in addition to the nuchal papilla situated in the posterior heart-shaped incision of the cephalic lobe, there are two invaginated lateral papillae slightly before the tentacular cirri. The nuchal organs have the most complicated structure in Notophyllum, in which they form paired elongate processes extending to the dorsal side of the body, sometimes to the 7th segment ("epaulettes"); there may be as many as 7 of these paired processes.

In the benthic Phyllodocidae, two or three of the anterior body segments adjacent to the cephalic lobe usually differ from the following segments in the structure of podial appendages. These anterior segments are usually named circumoral (peristomal) segments or tentacular segments, because they bear the tentacular cirri. One pair of elongate cirri tentaculares is present usually on the 1st segment — there are 2 pairs only in the general Eteone and Pelagobia; there are normally 2 pairs of these cirri on the 2nd segment; the podial lobe is much reduced and setae may be absent; the 3rd segment usually has dorsal tentacular cirri and well developed podial lobes, as well as normal ventral cirri. All three anterior segments are distinctly separated from each other, and differ little in size from the other body segments. There are, however, many species in which the boundaries between the anterior segments on the dorsal side of the body have disappeared and the segments are markedly reduced in length, i.e. they become partly fused. These modifications of the anterior segments are connected with a reconstruction of the nervous system: there is only one pair of large subpharyngeal ganglia, corresponding to the three anterior segments, which innervate all the tentacular cirri; in species with separated segments (Eulalia), the subpharyngeal ganglia have thin connections (p. 41). These are the beginning stages of cephalization — the formation of a distinct peristomium. The Phyllodocidae still do not have a distinct peristomium formed by the fusion of several anterior segments. Such a peristomium is present in higher errant polychaetes, the Aphroditidae and Nereidae. The cephalic part of Phyllodocidae has a much simpler structure. Some possible lines of development of a more complicated cephalic part are shown in Figure 2 (see the section "Phylogenetic relationships in the family Phyllodocidae").

The cephalic part of the Alcionidae differs little from that of the Phyllo-
26 docidae, but the modified anterior segments may be more numerous; the cephalic lobe of the Alcionidae is camouflaged by the hypertrophied telescopic eyes. The cephalic part of the Lacydoniidae has the same structure as in the Phyllodocidae, and the family was therefore grouped together with the Phyllodocidae in the past. The Tomopteridae and Typhloscolecidae have an unusual structure of the cephalic part: the cephalic lobe has become markedly reduced and fused with the anterior segments. The distinctive characters of the Tomopteridae are the very long tentacular cirri, the so-called "whiskers," and the cephalic lobe of the Typhloscolecidae ends in a characteristic, elongate, fingerlike appendage, the palpod. These structures are evidently adaptive and connected with the pelagic mode of life.

The organs of sight, usually a pair of dark spots, are situated on the posterior part of the cephalic lobe. The size of these dark spots varies considerably in the different species. They are sometimes so small and so deeply situated under the epidermis that they are difficult to recognize. Abyssal Phyllodocidae usually have no eyes, Austrophyllum, Vitiazia and others, like the abyssal Aphroditidae, Harmothoe derjugini, Pholoe caeca, Weberia nodulosa, most species of Macellicephala and Macellicephaloides, and genera of other families. Reduction of the eyes has also been observed in fossorial forms, which burrow into the ground. For example, the very small eyes of Eteone are scarcely distinguishable, and in species of the interstitial fauna (Hesionura (= Etionides)) the eyes have disappeared altogether (Hartmann-Schröder, 1964). The same applies to Lumbriconereis (Eunicidae).

In the Phyllodocidae, the eyes are situated below the cuticle and resemble a bubble, the walls of which consist of elongate prismatic cells which are particularly long on the lower side of the eye. These cells contain dark pigment and form the retina. The eye is filled with a transparent jellylike fluid, the vitreous body, which forms a lens in the center and is light-refracting (it is not present in all species). The eye is surrounded by branches of the short optic nerve, which is connected with the mesencephalon. The cuticle is usually without pigment where the eyes are situated. The eyes of the Alcionidae are of the same type, but their structure is more complicated (Greef, 1876b; Demoll, 1909); they are very large (telescopic) and are connected by muscles, which can change the direction of the axis of the eye and can apparently determine not only the intensity and direction of light, but also the outline and size of objects, which is of advantage to pelagic species as it enables them to survey the surroundings in different directions. The eyes of the Tomopteridae are very small and of different structure from those of the Phyllodocidae and Alcionidae. The eyes of Tomopteris have no vitreous body, and the light-refracting lens consists of epidermal cells (Åkesson, 1964).

Pharynx and methods of feeding

The intestine, which is usually a straight tube, begins at the mouth at the border between the cephalic lobe and the first segment and ends in the anus
27 at the posterior end. In species which swallow large quantities of silt, the intestine is considerably longer than the body and forms more numerous loops (Sternaspidae, Opheliidae and others). It is not connected with the body cavity and is suspended from mesenteries and protected against pressure by metameric septa, which contain radial muscles. The intestine consists of three main parts: the fore-intestine, a derivative of the stomodeum; the mid-intestine and the hind-intestine (proctodeum). The fore- and hind-intestine are ectodermal, the mid-intestine is endodermal.

The fore-intestine has a complicated structure: in addition to the pharynx, which protrudes to the outside, there may be distinct anterior and posterior ventricles in its posterior part (proventriculus and postventriculus) with muscular walls which have blind pockets which serve for respiration (e.g. in the Syllidae).

The pharynx is represented by two different types: 1) a saclike pharynx (ventral proboscis), a relatively short blind sac situated below the esophagus; 2) a tubular pharynx (axial proboscis), which passes gradually into the mid-intestine. The ventral proboscis is very specialized, and present in the errant polychaetes only in the Eunicidae and Amphinomidae; the second type (axial proboscis) is more common and is present in all other errant families. In sedentary polychaetes, both types are also present, but the pharynx is usually much reduced.

A long tubular pharynx is present in the Phyllodocidae and Alcionidae; the tubular pharynx is very short in the Tomopteridae, and in the Typhloscolecidae, due to their semiparasitic life, it is modified into a characteristic

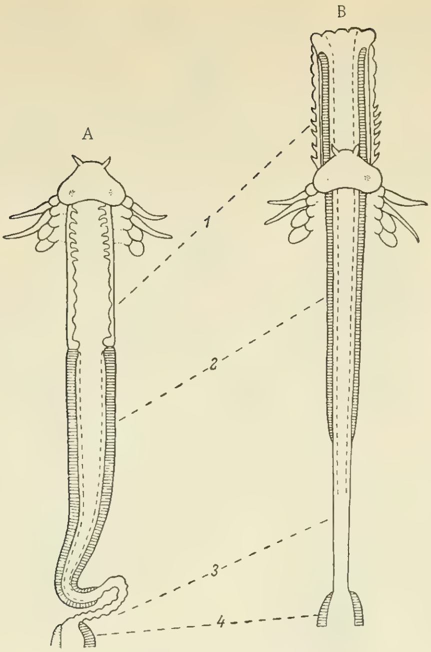

FIGURE 4. Fore-intestine retracted (A), and everted (B): 1) proboscis sac; 2) muscular part of pharynx; 3) posterior end of esophagus, or ventriculus; 4) mid-intestine.

suctorial organ. The pharyngeal apparatus of the Phyllodocidae consists of several parts. In addition to the small buccal cavity adjacent to the mouth, there are: 1) a "proboscis sac," the anterior part of the tube with thin soft walls, which forms the external integument of the proboscis when the pharynx is everted; 2) the middle, muscular part of the tube, which is the pharynx
29 proper; 3) the posterior part of the tube, with soft walls which can be markedly expanded or contracted; this part is named ventriculus (Figure 4).

Eversion of the pharynx, mainly by the pressure of the coelomic fluid moving from the posterior segments into the anterior segments, and the reverse process — invagination of the pharynx — take place by contraction of longitudinal retractor muscles. The pharynx is everted like the finger of a glove, and forms a long, mobile proboscis. The outside of the proboscis is usually covered with epithelial papillae, with gland cells the secretion of which possibly anesthetize the prey; in addition, the glands secrete proteolytic enzymes which promote digestion (Michel, 1968a). The innervation of the proboscis is very complicated; at its outer margin is a nerve ring, to which are connected four (Eteone) or six (Phyllodoce, Eulalia) main longitudinal nerve cords, with numerous anastomoses (Michel, 1965). According to V.K. Lebskii (1970), the proboscis of Eulalia viridis has, in addition to the 6 main nerves, 18 additional longitudinal nerve fibers (Figure 10). This makes the proboscis an extremely sensitive (tactile) organ, and because of its strong musculature, a strong instrument for

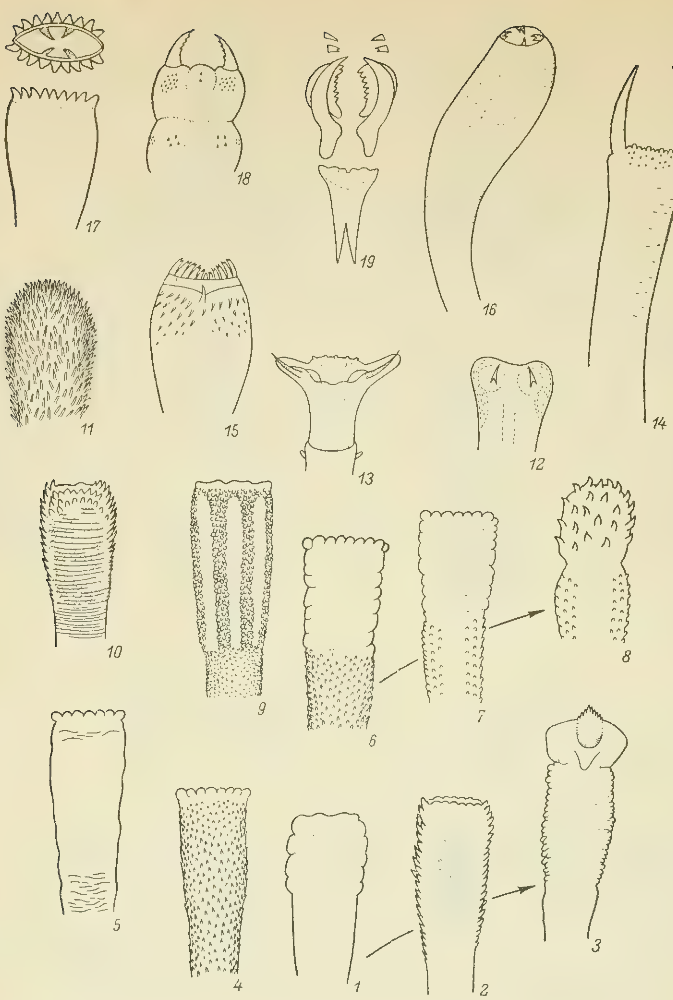

FIGURE 5. Proboscis of the Phyllodocidae and other errant polychaetes:

1) Eteone longa; 2) E. (Mysta) barbata; 3) E. (Mysta) tchangsii; 4) Eulalia viridis; 5) Eumida sanguinea; 6) Phyllodoce malmgreni; 7) P. (Anaitides) groenlandica; 8) P. (Anaitides) papillosa; 9) Austrophyllum charcoti; 10) Notophyllum imbricatum; 11) Pterocirrus macroceros; 12) Pelagobia longicirrata; 13) Phalacrophorus pictus; 14) Torrea candida; 15) Nephthys; 16) Glycera; 17) Harmothoe; 18) Nereis; 19) maxillary apparatus of Lumbriconereis.

catching food. The proboscis also has an important part in locomotion, particularly when the animals burrow into the ground, serving as an anchor and assisting in pulling the body.

The arrangement of the papillae on the proboscis, and their form, are of great importance for the determination of the species, and frequently of the genus. Figure 5 shows the main types of proboscis in the Phyllodocidae.

The figures illustrate the variety of forms of this organ. The pharynx of some errant polychaetes has been included for comparison.

The entire proboscis is uniformly (diffusely) covered with papillae in some Phyllodocidae, while in others the papillae are concentrated on specific areas on the proboscis. A diffuse distribution of the papillae should be considered as the more primitive pattern. The pattern of distribution of the papillae forms the basis for differentiation between the anterior (or distal) part of the proboscis and the posterior (or proximal) part. These two parts of the proboscis are most distinct in the central genus Phyllodoce.

The papillae at the entrance of the proboscis are the oral papillae. They form the "oral ring"; their number is strictly constant in some cases, but it may vary considerably. The form of the papillae on the outer surface of the proboscis varies markedly. In numerous species of Phyllodocidae, particularly in Pterocirrus macroceros, they are long and thin (finger-shaped), covering the surface of the proboscis so densely that it appears hairy. Similar long papillae have been observed in Pseudolacydonia caeca (Lacydoniidae), but in another genus of this family, Paralacydonia, the surface of the proboscis is smooth. More frequently the papillae form large, leaflike, pointed processes, or rounded warts arranged in more or less regular longitudinal rows. When the proboscis is incompletely everted, the folded (wrinkled) appearance of its walls may imitate papillae. The papillae are sometimes covered with small needlelike chitinous spines, which may be situated not on the papillae but on the surface of the proboscis. An extreme example of a proboscis with needlelike and hook-shaped spines is Glycinde (Goniadidae). The proboscis of Glycinde resembles the radula of molluscs (a peculiar convergence). In the Phyllodocidae, there are only two aberrant pelagic genera: Phalacrophorus and Pelagobia, in which there are small paired chitinous jaws on the anterior end of the proboscis. These jaws developed as adaptive structures connected with pelagic life, for catching rapidly moving planktonic organisms; they developed independently in the two genera, which belong to different subfamilies. In some Alcionidae, the distal part of the proboscis ends in very long cirriform appendages with numerous cells with a sticky secretion, also an adaptive structure for catching prey. The cirriform appendages of the Alcionidae show some analogy to similar structures in Macellicephaloides (Aphroditidae).

The proboscis as an instrument for catching food had a progressive role in the development of Polychaeta. A proboscis of strictly defined structure is characteristic for most errant families. Thus, it is covered with soft papillae on the outside in all Nephthyidae (Figure 5, *15*), and has two large inner chitinous teeth which hold the prey. The Polynoidae (Figure 5, *17*) have 4 large, black, hooked jaws in two pairs, one opposite the other and situated near the outer opening. The Glyceridae (Figure 5, *16*) have the strongest proboscis, longer than half the body, with four strong hooks arranged in a cross at the distal end projecting to the outside. The proboscis of the Nereidae (Figure 5, *18*), in addition to two curved distal hooks with a serrated cutting edge, which act like claws and sometimes like a rake, is covered on the whole surface with numerous small chitinous teeth, paragnathae, concentrated in "paragnathous groups." The jaws of the Eunicidae have a most complicated structure (Figure 5, *19*); they consist of the lower jaws, which form two plates with a calcified anterior margin and an elongate pedicel, and of the upper jaws which consist of 5 or more paired chitinous plates of different form and size. The proboscis of the Phyllodocidae is less complicated and its armature, which consists of soft papillae, is very variable.

Although the proboscis of most errant polychaetes is of a strictly defined structure, there are surprising cases of convergence. Thus, Berkeley (1963) described the proboscis of Lycastopsis catarractarum (Nereidae), which resembles that of the Phyllodocidae in that the soft papillae overlap like tiles or scales of spruce cones. This resemblance is due to the special food of these species and does not indicate relationship. In the section on the phylogenetic relationships in the family Phyllodocidae, we discuss cases of parallelism in the structure of the proboscis among the Phyllodocidae.

There are many different methods of feeding in the Polychaeta: all errant species are mainly predators, but filter-feeders also occur among the polychaetes — passive catchers of seston by means of a complicated catching apparatus (Sabellidae, Serpulidae), collectors of detritus from the bottom, 31 with the aid of the long tentacles (Terebellidae). Many species are soil-feeders or limnophagous, feeding on small organic particles in the silt (all fossorial forms). Forms which swallow soil indiscriminately have to be distinguished from species which actively select organic matter. The species which swallow soil indiscriminately feed mainly on bacteria, which are present in enormous numbers on the mineral particles of the bottom. The role of bacteria as food of polychaetes has been little studied. These indiscriminate soil-feeders are apparently not numerous; most limnophagous species have special adaptations, which are not well known and which help them to select organic detritus in the soil (for example, the sand funnel of Arenicola is situated only in the superficial layer of the ground, which is richest in detritus).

The Phyllodicidae are mainly active predators which ambush their prey; the prey may be larger than the predator, which catches it with the rapidly everted proboscis. Remains of different organisms have been found in the stomach, including tentacles of polychaetes of different families. The tracking and attack of a large specimen of Spio filicornis by Eteone longa in the littoral of the Kuril Islands was observed by V. V. Khlebovich (1959).

Cases of cannibalism have been recorded (Gravier, 1896) among the Phyllodocidae (Eulalia viridis, Eumida sanguinea, Phyllodoce laminosa); E. viridis in the White Sea practices selective cannibalism: males attack males, but never females; females attack males, but never other females (Buzhinskaya and Lebskii, 1971). Cannibalism has been observed also in other polychaetes; it is especially common in the Nereidae (Reish and Alosi, 1968). Nereidae sometimes behave "perfidiously": a male and female of Nereis caudata first build together a tube of mucus with lateral windows for ventilation, then, after the female has deposited eggs in the tube, the male devours her. The male, however, takes care of the progeny and ensures constant washing of the eggs with new water by movement of the parapodia (Herpin, 1923).

If animal food is absent, Phyllodocidae also feed on plants (fragments of seaweed have been found in their intestine). The same has been observed in Nereis (Beklemishev, 1950). Mixed food is probably widespread among polychaetes. The daily feeding of the Phyllodocidae has not been studied, and it is not known whether a rhythm of feeding exists which has been observed in Harmothoe imbricata (Strel'tsov, 1966a, 1968). Some polychaetes, particularly Phyllodocidae, can stand prolonged starvation, but they apparently utilize amino acids dissolved in the water in such cases, as has been proved for Nereis (Taylor, 1969).

Judging from their behavior and their strong proboscis, the Alcionidae are active predators, but there are no direct observations. They are assisted in the search for prey by their telescopic eyes, which enable them to orient themselves in different directions (up, down), as well as to recognize the size and form of the prey. The Tomopteridae have a very short pharynx, but they are voracious predators. Remains of herring fry, fragments of
32 Agalmopsis elegans (Siphonophora) (Åkesson, 1962) and of Oikopleura dioica (Appendicularia) (Rakusa-Suszcewski, 1968) have been found in their intestine. According to Rakusa-Suszcewski, Tomopteris helgolandica in the Atlantic Ocean mainly attacks Parasagitta elegans and Sagitta setosa, making holes in their body through which the predator sucks the body fluids; remains of Sagitta have been found only rarely in the intestine of Tomopteridae. The Typhloscolecidae, which have a characteristic suction apparatus instead of a proboscis, should obviously not be considered as predators, but rather as semi-parasites (p. 51).

The Phyllodocidae, which are active predators, are often attacked by other worms. Thus, remains of the free-living Eteone have been found in the stomach of the tubicolous Diopatra cuprea (Mangum, Santos and Rhodes, 1968). Phyllodocidae also feed on various fishes, including commercial species (Ushakov, 1955a).

Parapodia and the character of locomotion of Polychaeta

The lateral processes of the body, parapodia, which are covered with numerous setae, are complicated structures with several functions, mainly, however, as organs of locomotion, acting as levers. In addition to the podial cirri, which have mainly a tactile function, special branchial appendages (coelomic in the Glyceridae, with a rich supply of capillaries in the Eunicidae) are present on the parapodia, and also papillae, ctenidia, stylodes, etc., the function of which has not been determined so far; there are sometimes also small light-sensitive eyespots on the parapodia (Opheliidae). Closely connected with the parapodia is the excretory system, nephridial papillae (nephropores), usually on the ventral side of the parapodia. Genital products often develop in their cavity.

The parapodial complex is of markedly different structure in the different families, which is connected with the specific ecology and the general degree of complexity of organization. Parapodia are very plastic and adaptive organs. Their narrowly adaptive character, mainly to locomotion, is clearly reflected in the structure of the podial complexes.

The movements of polychaetes are of different types. There may be slow crawling or swimming, rapid active flight, burrowing into the ground and rapid retraction into their shelters, tubes, in which some species spend a large part of their life. Polychaetes which live in tubes firmly attached to the substrate and are unable to leave them are sedentary or sessile.

The following methods of locomotion are distinguished: sinusoidal, or serpentine, i.e. undulate bending of the body parallel to the substrate (characteristic for the benthic Phyllodocidae), rowing with the parapodia

(Alcionidae and Tomopteridae), and peristaltics, or "hydraulic movement" (Zenkevich, 1944); the last is characteristic for many fossorial forms. Combining of several methods of locomotion is common.

33 Benthic Phyllodocidae move over a hard substrate usually by sinusoidal movements. In addition to the curving of the body horizontally, the action of the podial appendages with their setae which act like paddles is very important. The Nereidae move by the same method. Sometimes, in rapid motion, benthic Phyllodocidae detach themselves from the substrate and swim for brief periods. This is done more easily by Nereidae, as the surface of their parapodia is larger.

Before they begin to move, benthic Phyllodocidae extend the anterior end alternately in different directions, as though searching with the tactile appendages and organs of sight for the direction (Bohn, 1906). Only afterwards does the worm begin to make bending movements of the body which spread from the posterior to the anterior end; the cephalic end acts as the steering mechanism which determines the direction of movement. If the animal is excited, the length and amplitude of the waves of the body increase markedly and the speed of forward movement increases. Mucus secreted facilitates gliding over the substrate, and protects the delicate integument from injury. During the undulate movements in the horizontal plane, the parapodia on the inward-curved side of the body decrease in size by contraction of longitudinal muscles, the setae are partly retracted, and the entire parapodial complex is brought forward. At the same time, the podial appendages on the opposite, outward-curved, side markedly increase in size, the setae are projected outward to the maximum, so that the working surface of the parapodium increases, and it makes a jerk posteriorly. During sinusoidal movement, the coelomic cavities on both sides of each somite contract consecutively and expand. A single wavelike curve of the body normally extends over 10 or more segments. When the movement deviates from the straight line, the symmetrical bending of the body becomes asymmetrical. Sinusoidal locomotion has been described in detail by Gray (1939) for Nereis. Direct observations of the behavior of polychaetes in nature, speed of movement, reaction to stimuli, etc. are unfortunately very few, and this makes it very difficult to understand the functional significance of many complicated structures.

The parapodia of Nereis are often considered as a "classic" example of the structure of the parapodia of errant polychaetes (Figure 6, *15*). The parapodia of Nereis consist of an undivided basal part and two branches: an upper, dorsal branch, or notopodium, and a lower, ventral branch, or neuropodium, each branch with a bundle of segmented setae (with mobile distal part) and supported by a large internal seta, the aciculum, which is usually dark brown or almost black. The aciculum forms the axial skeleton of the parapodium. Numerous muscle fibers extend from the lower part of the aciculum to the base of the external setae and to the wall of the parapodium. When the retractor and protractor muscles contract, the setae are partly retracted or they project outward. The dorsal and ventral branches
35 of the parapodia are provided with a dorsal and a ventral cirrus. The notopodium also has two, and the neuropodium one, elongate podial lobes, the ligulae, and the lobe of the neuropodium is covered by a small lip. All these formations markedly enlarge the transverse "rowing" surface of the parapodium. In some tropical Nereidae, (Dendronereis, Dendronereides), branched gills are present on the anterior segments, near the dorsal cirri; they consist of a large number of elongate processes. With the beginning of

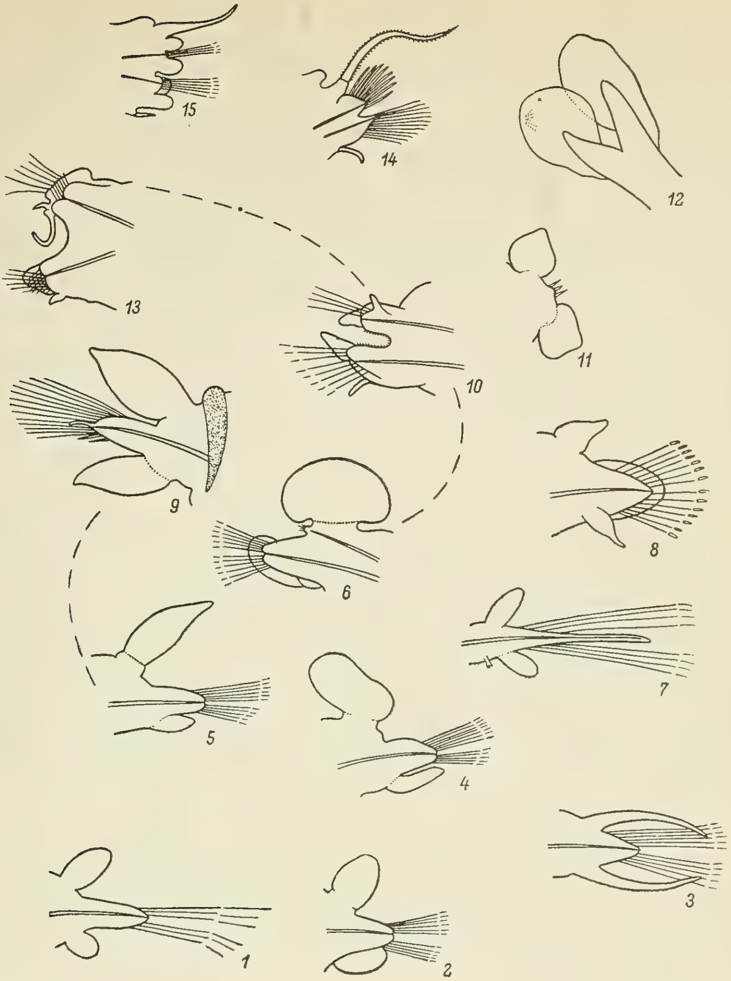

FIGURE 6. Parapodia of Phyllodocidae and some other errant polychaetes:

1) Protomystides; 2) Eteone; 3) Pelagobia; 4) Phyllodoce; 5) Eulalia; 6) Notophyllum; 7) Pontodora; 8) Lopadorhyncus; 9) Krohnia (Alciopidae); 10) Paralacydonia (Lacydoniidae); 11) Travisiopsis (Typhloscolecidae); 12) Tomopteris (Tomopteridae); 13) Nephthys (Nephthyidae); 14) Harmothoe (Aphroditidae); 15) Nereis (Nereidae).

maturity and epitoky, the parapodia of Nereidae usually undergo considerable morphological changes, so that the sexual stages of this family were originally described as a different genus. In particular, the eyes of mature forms are hypertrophied, histolysis takes place in some tissues, and all podial lobes become markedly enlarged; the old setae are replaced with others, the so-called natatorial setae, with a broad distal segment. All these modifications help the worm to rise to the surface and lead a pelagic life, during which the sexual products are deposited (these stages are named heteronereid).

The type of biramous parapodia described above for the Nereidae is found, although rarely, in polychaetes which have notopodia and neuropodia of similar structure. The parapodia of Nephthyidae are to some extent of analogous structure (Figure 6, *13*). In the Aphroditidae, the neuro- and notopodia are of different structure (Figure 6, *14*; also p. 37). Complicated modification takes place in the parapodia of sedentary worms which live in tubes. Narrow specialization, connected with the tubicolous mode of life, is evident in the parapodia of these species. The dorsal and ventral branches are markedly distant from each other, and the neuropodia are modified into transverse ridges (torus uncinigerus) with one or several rows of small serrated plates (uncini), used for attachment to the walls of the tubes. If both branches of the parapodia are situated on a common stem, which is the case in most errant polychaetes, parapodia are named monostichous; if the dorsal and ventral branches are distant from each other and modified, they are named distichous.

In addition to parapodia of complicated structure, there are also simple, uniramous parapodia, with a single podial lobe, bearing only one aciculum and one bundle of setae. Uniramous parapodia are found in polychaetes more rarely than biramous parapodia with a neuropodial and notopodial branch and two bundles of setae, which apparently perform some functions of the parapodia more effectively. Uniramous parapodia are present in the Sphaerodoridae and many species of Syllidae. The Syllidae may have parapodia of a transitional type, so-called pseudobiramous parapodia, with an additional notopodial aciculum, but without a separate bundle of dorsal setae; fine hairlike notopodial setae appear on them only at the beginning of maturity, facilitating the rise to the surface. Parapodia of many species of Eunicidae have several acicula, but there is no distinct differentiation into notopodium and a neuropodium. The parapodia of the Glyceridae are either uniramous or biramous.

Uniramous parapodia are characteristic for the Phyllodocidae; they have one podial lobe with a single aciculum and one bundle of setae (Figure 6, *1-5*). The parapodia of benthic Phyllodocidae show little modification. The
36 podial lobe is usually extended and has a shallow depression at the distal end in which the aciculum is situated. The aciculum is usually of light color and weaker than in the Aphroditidae and Nereidae; its weak development is due to the fact that the external setae are very thin and not differentiated.

The podial lobe of the Phyllodocidae bears a dorsal cirrus and a ventral cirrus, which is markedly flattened and leaflike in form. The ventral cirri, which project from the ventral side of the podial lobe, are usually shorter than the lobe. The dorsal cirri are displaced to the dorsal side and are usually situated on pedestals, the cirrophores, which are evaginations of the body wall; the cirrophores give considerable mobility to the dorsal cirrus. It is important to note that in the most primitive genera of Phyllodocidae, e.g. Lugia and Protomystides, cirrophores are practically absent and the cirri are apparently situated directly on the dorsal surface of the body. The dorsal cirri are broadly oval, heart-shaped or lanceolate, often with a pointed end. They partly overlap and partly cover the sides of the body like tiles, like the elytra of the Aphroditidae.

The dorsal and ventral cirri of the Phyllodocidae contain numerous gland cells, which secrete abundant mucus; they are also supplied with densely branching nerve endings, which shows that they have a tactile function. The dorsal cirri are in constant rhythmic movement (beating), even when the worm is not moving; they cause thereby water to flow over the body. This proves that the dorsal cirri of the Phyllodocidae are not only tactile organs, but also ensure respiration to some extent.

Only a few Phyllodocidae, Austrophyllum, Hesporophyllum, Notophyllum, Nipponophyllum and Zverlinum, have at the base of the dorsal cirrus an additional aciculum and one or two small hairlike notopodial setae; they may be present on all segments, or only on the posterior segments. The presence of a notopodial aciculum should be considered as the first stage of development of biramous parapodia. An additional notopodial aciculum has been observed in the Phyllodocidae only in genera in which the anterior segments have become more or less fused, i.e. in which the process of cephalization has begun, but not in the primitive forms with only slightly modified circumoral segments. In the families dealt with here, typical biramous parapodia are present only in the Lacydoniidae (Figure 6, *10*), which used to be included in the family Phyllodocidae. The parapodia of the Lacydoniidae resemble those of the Nephthyidae in some characters (Figure 6, *13*).

The parapodia of the Alcionidae resemble the type described above for the Phyllodocidae, but because of their planktonic mode of life, the dorsal cirri are as large as the ventral, and the very long, fine setae are more numerous, which apparently facilitates floating in the water (Figure 6, *9*).

In the small aberrant pelagic Typhloscolecidae, the podial lobes are almost completely reduced, and only one or two small, short, needlelike setae are present; on the other hand, the dorsal and ventral cirri are hypertrophied and have the form of broad plates, which promote the maintenance of a vertical position in the water (Figure 6, *11*). An even more extreme adaptation to floating has developed in the Tomopteridae (Figure 6, *12*): the setae have disappeared, except on the cirri peristomiales of the 2nd segment ("whiskers"), and the very large, bilobed podial processes at the distal end
37 bear special fins (pinnules). It is not clear whether these fins are homologous with the dorsal and ventral cirri.

Which type of parapodia, uniramous or biramous, is more primitive will be discussed below (p. 35).

Setae

Setae are the main armature of the parapodia; they are present on all body segments (except in the Tomopteridae). Setae of marine Polychaeta are very diverse in form and structure, often giving systematic characters for determination of the family, genus and species. A distinct composition of setae is characteristic for most families. There are two main types of setae: simple setae, which consist of a single part, and segmented setae, which consist of two parts: the shaft, or the main stem, and the distal part, which is articulated with the shaft. If the denticles which connect the shaft with the distal part are of uniform size, the setae are named homogomph, if they are of different length, they are named heterogomph. It is not possible or necessary to describe all the varieties of setae, many of which have been given special names because of their specific form: hairlike, spine-shaped, needlelike, aristate, pubescent, feathered, pectinate, harpoonlike, bayonet-shaped, beaklike, hook-shaped, hoelike, etc. The setae of sedentary worms are the most diversified, and may be different in the different parts of the body. Particularly modified are the setae on the anterior segments of sedentary species, rarely on the posterior segments (e.g. on the scapha of the Pectinariidae). Modified setae on the anterior segments sometimes have the appearance of a plume (Stylarioides), sometimes the form of an open fan (Pectinariidae, Ampharetidae), or of a rounded lid which covers the entrance of the tube (Sabellariidae). Large, slightly curved, golden setae, named palea, on the anterior end of Pectinaria, act like a harrow or rake when the worm with its tube moves in the ground (Wilcke, 1952). A large variety of setae is found in the Eunicidae, which live in tubes. In particular, in Rhamphobrachium, the tubes of which are situated deep in the ground, the first three anterior segments bear exceptionally long setae with a hook-shaped distal end and numerous lateral spines. If retracted, the setae extend in the body to the 30th segment or even farther (Berkeley and Berkeley, 1938). They evidently form a specialized catching apparatus, which draws organisms stuck to them and detritus toward the mouth, much like the tentacles of the Terebellidae. Such deeply retracted setae are not known in other polychaetes.

One type of setae is characteristic for the Phyllodocidae — segmented
setae, with a long distal part (Figure 7, *1*). There are 20—30 setae in a
bundle, but sometimes many more. The setae are situated on the posterior
side of the podial lobe in an arc, resembling a horseshoe. They form
a slightly concave fan. Behind the main vertical row of large setae, younger
38 setae, which replace the old, form the second row. The ventral setae are
usually shorter than the middle and dorsal setae, so that practically all the
setae run out simultaneously during crawling; they mainly act as hooks, the
distal part providing a large area of support (analogous to the tarsi of insects);
some of the dorsal setae possibly act as paddles during rapid movement.
The form of the setae is the same on the whole body. The undifferentiated
setae of the Phyllodocidae indicate the primitiveness of their parapodia. On
39 the biramous parapodia, the setae on the dorsal and ventral branches are
usually of different types and are often different in the same bundle, which
proves a further complication of the podial complex.

The main shaft of the setae in the Phyllodocidae ends in a slightly broadened rostrum, which usually has two large denticles at the articulation with numerous small spines. The distal part is usually long and thin, spear-shaped or saber-shaped, finely serrated on the inner side, which is slightly concave and turned downward, and smooth on the outer margin. The distal part is movable. In the pelagic Lapadorhynchus (Figure 7, *3*), the distal part of the setae is markedly widened, forming an oblong, flattened plate; setae of this type enlarge the surface of the body, which is important for floating in the water and evidently act as paddles during swimming: they move forward with the margin and backward with the whole surface. Lapadorhynchus has also simple hook-shaped setae (Figure 7, *4*), which are large on the first 3 markedly modified and widened anterior segments. This type of setae possibly holds the prey. Similar simple, hook-shaped, golden setae are found among the benthic Phyllodocidae only in Chaetoparia (Figure 7, *2*).

During epitoky, connected with the beginning of maturity, additional long, simple setae may develop in some benthic Phyllodocidae to facilitate their rise to the surface. For the Alcionidae, simple, long setae and segmented setae are equally characteristic; small, short, spine-shaped setae are

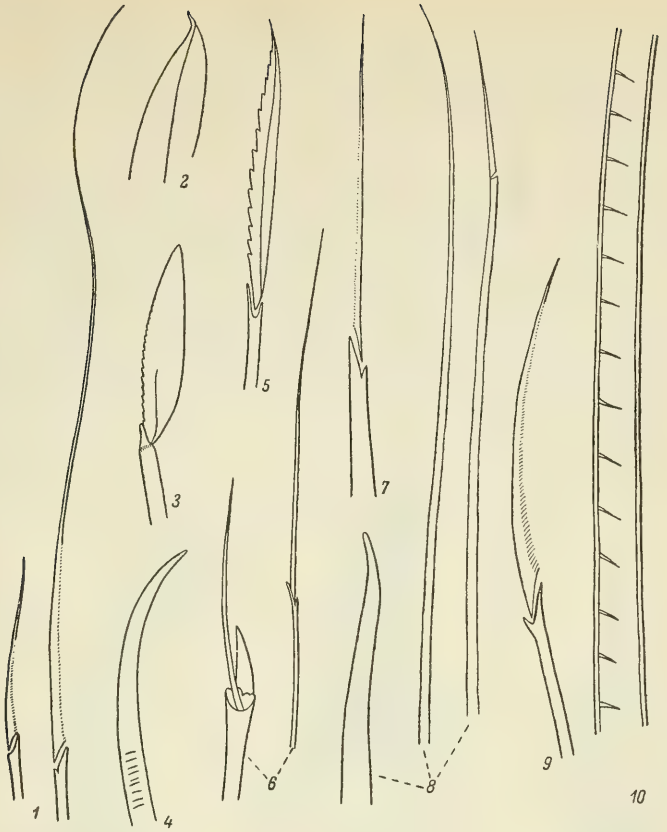

FIGURE 7. Types of setae:

1) segmented, or articulated, setae with a short and a long distal part in benthic Phyllodocidae (Mystides); 2) hook-shaped, golden seta on the anterior segments of Chaetoparia; 3) segmented seta with a broad distal part in Lopadorhynchus; 4) hook-shaped seta on the anterior segments of Lopadorhynchus; 5) segmented seta of Pelagobia, with a serrated distal part; 6) thick and thin segmented setae of Maupasia; 7) segmented seta of Pontodora with a thin distal part; 8) spine-shaped, simple, hairlike, and segmented setae of the Alcionidae; 9) segmented seta of Paralacydonia; 10) inner structure of axial seta of Tomopteris.

characteristic for the Typhloscolecidae. The Tomopteridae have a single pair of very long setae enclosed in the tentacular cirri of the 2nd segment; These setae have internal septa which gives them some flexibility. Figure 7 shows the main types of setae in the species of the families dealt with in this work.

It should be remembered that conventional microscopes do not permit detailed study of the fine structure of the setae, particularly, of details of the structure and serration of the rostrum, which may prove of great importance for the identification of species and lower taxonomic units. The use of the electronic scanning microscope will probably give much new information. The drawings of the setae of Phyllodocidae are usually very diagrammatic and not exact; this applies also to the present work. The (relative) length and width of the distal part is of systematic importance, but this has usually not been exactly described. However, the setae of abyssal species have a very long distal part, which may facilitate movement over soft silt.

The formation and growth of the setae have been studied in detail by Bobin (1944) in different families of polychaetes, including Eulalia viridis. The setae of all polychaetes develop in setigerous follicles, which are invaginations of the epidermis; uniramous parapodia have only one setigerous follicle. The setigerous follicles are lined inside with a membrane and contain a number of follicules, large basal cells the secretion of which forms the setae (formative cells). These basal cells are normally surrounded by connective tissue cells, which have no part in the formation of setae. Each basal cell develops one seta.

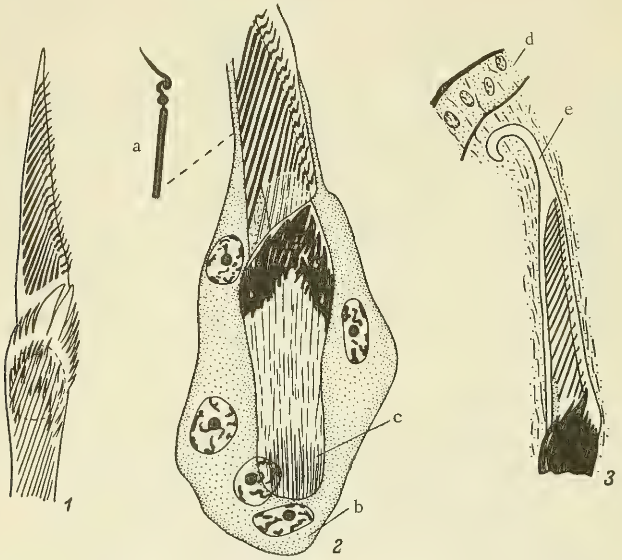

FIGURE 8. Structure and formation of the setae in Eulalia viridis (after Bobin, 1944):

1) structure of developed seta; 2) beginning stage of formation of the shaft of the seta; 3) distal part of a young seta under the epidermis; a) detail of serration of the distal part; b) basal cell; c) ciliary apparatus; d) epithelium; e) vacuole, in which the distal part of the seta is enclosed.

Near the setigerous follicle is a generative zone which produces new basal cells, ensuring the development of new setae to replace those discarded. The basal cells have a large nucleus and a vacuole, which the seta develops. According to Bobin, the basal cells have a special "ciliary apparatus" with numerous blepharoplasts. The number of blepharoplasts increases during the growth of the seta. The blepharoplasts in the middle of the "ciliary apparatus" are larger than those on the periphery. The blepharoplasts project

fine fibrils into the cell ("rhizoplasts"), which become intertwined and form the base of the seta; the blepharoplasts also send upward a single fibril or several fibrils grouped together, which resemble the membranellae of Infusoria; these fibrils become agglutinated with a protein base and form the shaft of the seta, which retains the fine internal structure (striation) connected with the presence of the "ciliary apparatus." In the development of segmented setae, the distal part is formed first, and the "ciliary apparatus"
41 of the distal part is replaced with a new "ciliary apparatus" (not connected with the first), which forms the shaft. Figure 8 shows the first stages of formation of the setae in Eulalia viridis. The distal part penetrates through the epithelium only when it is completely formed.

There is little information on the chemical composition of setae. The refraction of light by the fibrils of the setae resembles that of the chitin of Crustacea and insects; chitin forms 1/3 to 1/2 of the dry weight of the setae. In the Amphinomidae, the setae are impregnated with lime and very brittle. Many setae are transparent, colorless (particularly in the Phyllodocidae), but often have a golden sheen; the long setae of Aphrodite hang down from the sides of the body, iridescent in all colors of the rainbow, from sky blue to emerald green and from dark golden to ruby red.

On the primitive character of the uniramous parapodia

Which type of parapodia, uniramous or biramous, is more primitive in the recent Polychaeta? This is of great importance for the construction of a natural classification of numerous families, but it has been little discussed. Most authors think that the uniramous parapodia of recent polychaetes developed from biramous parapodia by reduction of the notopodium. This view was developed by Bergström (1914, p. 85), who thought that the primitive Annelida had numerous acicula, like the recent Eunicidae, which he considered as primitive. In his opinion, two of the acicula became differentiated only later, forming biramous parapodia, and still later, particularly in the Phyllodocidae, the notopodium was reduced, resulting in uniramous parapodia. Bergström based the whole classification of the Phyllodocidae on this view, and placed first the genus Notophyllum with an additional notopodial aciculum. However, in the specialized genus Notophyllum (see the section on phylogenetic relationships in the Phyllodocidae), the cephalization of the anterior segments has progressed much further than in other genera of Phyllodocidae, and it can therefore hardly be considered as the ancestral genus of the family. The acicula and the external setae have the same origin. However, the internal setae of the primitive Annelida cannot be compared with the acicula of the recent Eunicidae. The acicula are the axial skeleton of the parapodia which control the movement of the external setae, and become formed only after the formation of a complicated bundle of external setae. The number of acicula depends on the structure of the bundle of external setae. The external setae probably became differentiated only gradually, and the axial apparatus of the parapodia therefore became complicated also gradually. One aciculum is sufficient to control all the setae in the more primitive forms with a weak bundle of fine setae, as in the Phyllodocidae. When the bundle of external setae became complex, a stronger aciculum became necessary, and when the setae had become

42 differentiated and different setae had different functions, one aciculum was no longer sufficient, and further acicula developed. The presence of numerous acicula in the recent Eunicidae does not indicate their primitive character, but is due to the development of a complex set of specialized setae. In later works, the uniramous parapodia of the Phyllodocidae were also considered to have developed by the reduction of the notopodium (Fauvel, 1923; Day, 1967). Livanov (1955, p. 136) writes on this problem, rather vaguely: "...biramous parapodia ... are the usual condition of recent polychaetes, and the cases in which the parapodia are primitive, uniramous, are usually caused by reduction of the notopodium, as in the Eunicidae."

The problem of the primitive type of parapodia has been recently discussed by V. Storch (1968), who bases his phylogenetic classification on the theory of the primitive character of the Amphinomidae (p. 69). He considers the biramous parapodia of the Amphinomidae — Aphroditidae as the primitive type, because the protective, or defensive, role of the notopodia, which is very clear in the Amphinomidae, is one of the primary functions of the parapodia. Storch draws an analogy with the protective structures of primitive molluscs, particularly with the spines of *Solenogastres* and the dorsal scales (scutella) of *Chiton*. This does not seem very convincing, since dorsal protective formations developed in molluscs because of their slow crawling, while the primitive Annelida probably escaped from their enemies by rapid movements. In our opinion, the protective role of the parapodia is secondary and additional, and developed only in a few polychaetes. The notopodia cannot be considered only as protective adaptations, their function is much more complex. The parapodia of the Amphinomidae have a very complicated morphology, and are highly specialized, with hardly any primitive characters.

The simplest parapodia in the recent errant polychaetes are those of the benthic Phyllodocidae (p. 31). Their uniramous parapodia did not develop by a regressive process (reduction of the notopodium), but are the primitive condition of these organs. In the ontogenesis of benthic Phyllodocidae, the beginning of development of the parapodia in the form of two or several primordia has never been observed (their nectochetes always have a single bundle of setae). The primitive character of the uniramous parapodia in the Phyllodocidae agrees well with numerous other primitive characters in their structure, described in detail in this work. We therefore believe that the primitive type of parapodia in polychaetes is the uniramous parapodium. Biramous parapodia, which are typical for most marine Polychaeta, developed in connection with the general complication of the ecology of polychaetes. This took place because of the gradual diversification of functions of the parapodia, in addition to locomotion. In some cases, uniramous parapodia could of course have developed from biramous parapodia by reduction of the notopodium, so that not all uniramous parapodia of recent polychaetes are necessarily primitive. However, a regressive process has not been
43 observed in the Phyllodocidae. On the contrary, closely connected with the first stages of cephalization, a parallel process of the formation of developing notopodia in the form of additional acicula of the notopodium can be observed in this family.

The diversity of function of the parapodial complex is evident in *Harmothoe* and *Nereis*. Compared with the Phyllodocidae, the parapodia of these genera have more complicated functions. The parapodia of *Harmothoe imbricata* are typically biramous, with sharply differentiated and widely separated neuropodium and notopodium (Figure 6, *14*). This species does not burrow into the silt, and moves on the surface of the substrate only with the help of ventral setae, which function as stilts (a method of locomotion named "marching"). The dorsal podial branches bear numerous large, straight or slightly curved setae directed upward in the form of a wide fan. These setae take no part in movement. Their function is the maintenance of the "respiratory canal" under the elytra, in which eggs are often carried which require constant renewal of water. These notopodial setae support the elytra, maintaining an empty space under them and protecting the "respiratory canal" at the sides of the entire dorsal side from becoming clogged by particles; they are a "ventilation grating." The integument of the Phyllodocidae, through which respiration takes place, is protected against clogging by a "mucous case" (p. 14). The Aphroditidae, which lead a more active, mobile life, do not secrete much mucus and have therefore to rely on additional mechanisms to maintain gas exchange — "ventilation grating" mentioned above. The notopodial setae apparently have no defensive function: if attacked, the worms often shed the elytra and escape. In the commensal Aphroditidae, e.g. in Arctonoe vittata, which inhabits the mantle cavity of molluscs, the notopodia are weakly developed and there are few or no dorsal setae. This may be due to the fact that there is no need to protect the "respiratory canal" from clogging because the mollusc does this for them.

The structure of the parapodia in Nereis has been described in detail above (p. 28). Both podial branches act together as motor levers, which enables them not only to move rapidly on the ground, but sometimes also to swim upward. The podial lobes of the notopodia are even larger than on the neuropodia. This is to some extent related to and consolidated by epitoky, which is typical for the Nereidae. During the epitoky, when spawning takes place, the worms change from the benthic to a pelagic mode of life. At this time, they undergo considerable morphological modifications, particularly, a marked enlargement of the podial lobes, which enables them to swim rapidly in the surface layers of the sea. But it is not only for swimming that they need large notopodia. When immature worms are inside their V-shaped burrows in compact silt, sometimes 10—15 cm below the surface, they must make strong, twisting dorsoventral movements to ensure irrigation (aeration) of the shelters. Such movements can be observed if Nereidae are
44 placed in glass tubes, in which they remain alive for a long time. These movements drive freshwater through the long galleries. During these hydrokinetic movements, the function of the parapodia changes, from locomotion to fixation. The neuropodia and notopodia are used for "fixing" the worms on the same place. In the burrows, Nereis shows such a hydrokinetic activity almost continuously. Definite rhythmic movements of driving water through the tubes have been observed in some sedentary worms (Wells, 1951; Wells and Dales, 1951).

A weak development of the notopodia and absence of notopodial setae are characteristic for species of Lycastopsis. L. augeneri in Pos'et Bay in the Sea of Japan lives among loose remains of Zostera and other macrophytes thrown up on the shore, and does not make deep, narrow passages in compact ground (Buzhinskaya, 1967). The absence of well developed notopodia may be due to the fact that there is no need for constant ventilation. Moreover, epitoky has not been observed in Lycastopsis. Thus, various complications of the parapodia find their explanation in a specific mode of life. It should be stressed that Lycastopsis is more primitive than all other Nereidae in the structure of the proboscis.

Extensive data on the structure of the parapodia in polychaetes and their comparative evolutionary aspect have been given by Binar and Jeener (1930), who described numerous interesting complications of the parapodial complexes. The authors described some basic trends in the development of the parapodia. We consider the forming of a "highly developed group" of errant polychaetes: Phyllodocidae — Glyceridae — Nephthyidae as artificial. Their only reason for this grouping is that the proboscis takes an important part in the movement of these species. It is difficult to find a direct connection between the action of the proboscis as a "pulling instrument" and the structure of the parapodia. The proboscis of the Phyllodocidae takes a much smaller part in locomotion than the proboscis of the Glyceridae, which is larger and stronger than in the Phyllodocidae, but the notopodia are well developed in the Glyceridae but absent in the Phyllodocidae. However, the functional significance of some morphological formations of polychaetes has been far too little studied.

Metamerism of the internal organs

The external segmentation of the body usually corresponds to the internal metamerism, which is formed by internal transverse septa or dissepiments, which separate the somites, or metameres. The septa which isolate the coelomic fluid of the metameres have partly a protective function after injury of the body wall; if the worm is cut into two parts, it does not necessarily die. Regeneration of lost parts is well developed in polychaetes, and this is sometimes a precondition for asexual reproduction by division or budding, which always alternates with sexual reproduction (e.g. in the Syllidae); asexual reproduction does not take place in the Phyllodocidae (p. 42).

45 The basic internal organs, musculature, blood vessels, nerve plexuses and organs of secretion, are usually repeated in each body segment.

Musculature. This is well developed in the benthic Phyllodocidae, in connection with their sinusoidal movements (Figure 9). Under the basal membrane of the cutaneous epithelium are circular muscles which, however, do not form a continuous layer in polychaetes: they are usually weakly developed between the segments and interrupted by the parapodia on the sides. Of greater importance are the dorsal and ventral longitudinal muscles. The dorsal longitudinal muscles are better developed than the ventral in the Phyllodocidae; they form a continuous thick band on the entire dorsal surface. This is reversed in the Aphroditidae: the ventral longitudinal muscles are stronger than the dorsal, which is due to the different method of locomotion (p. 37). There are in addition dorsoventral muscles in each segment, situated before and behind the septa, and also oblique-ventral and lateral muscles, which move the parapodia.

The vascular system of Polychaeta is closed, consisting mainly of dorsal and ventral longitudinal vessels situated in the dorsal and ventral mesenteries. The dorsal and ventral vessels in each segment are usually connected by circular, or commissural, vessels, which give off a network of capillaries to the parapodia. The blood flows from the ventral trunk to the periphery (parapodial branchiae, if present), and the dorsal vessel receives blood from the periphery. The network of blood vessels in a segment is usually named angiosomite (Timofeev, 1923, 1924, 1930). The vascular system of

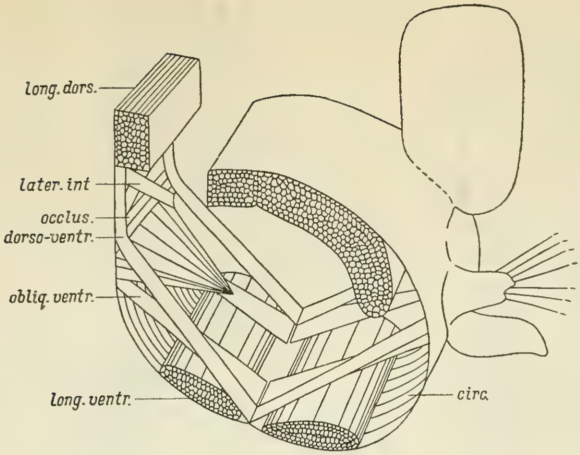

FIGURE 9. System of muscles in a somite of Phyllodoce groenlandica (after Storch, 1968):

long. dors. — dorsal longitudinal; later. int. — lateral internal; occlus.— adductor; dorso-ventr. — dorsoventral; obliq. ventr. — oblique-ventral; long. ventr. — ventral longitudinal; circ. — circular.

46 the Phyllodocidae is weakly developed; the lateral branches of the dorsal and ventral vessels do not form a closed system, and it is hardly correct to speak of an angiosomite in this case. The dorsal vessel is surrounded by longitudinal muscles and passes in the dorsal median line; the ventral vessel is situated free in the body cavity along the nerve cord, forming undulant curves. Gravier (1896) observed the movement of blood in the dorsal vessel, from the anterior toward the posterior end. However, there may be no constant direction of the blood flow in the Phyllodocidae. The blood of the Phyllodocidae (and of the Aphroditidae, Glyceridae and Syllidae) is colorless, and the hemoglobin is dissolved in the nerve tissue. The hemoglobin is used not for transporting oxygen in the Phyllodocidae, but for binding it in tissues which are very sensitive to a deficiency. The vascular system has mainly trophic functions, the distribution of nutrient substances. All these characteristics of the vascular system stress, according to Livanov (1940), the primitive organization of the Phyllodocidae: there are no specialized respiratory organs (gills) in the Phyllodocidae and related families, and the gas exchange is carried out by the entire surface of the body. To ensure the gas exchange, the Phyllodocidae have to make continuous respiratory movements with the whole body and with the dorsal cirri; the higher polychaetes, which have respiratory organs in the form of branched gills with a rich network of capillaries, do not need to make respiratory movements.

Nervous system. This is represented in polychaetes by the ventral nerve cord, which forms a complex of nerve endings, the neurosomite, in each somite. Each neurosomite consists of a ventral ganglion and 3 peripheral nerve rings, of which the anterior and the posterior control the movements of muscles, according to Livanov (1924), and the middle nerve ring, which forms the podial ganglion, is mainly a receptor; according to Bullock and Horridge (1965), the exact function of the nerve rings has not been definitely

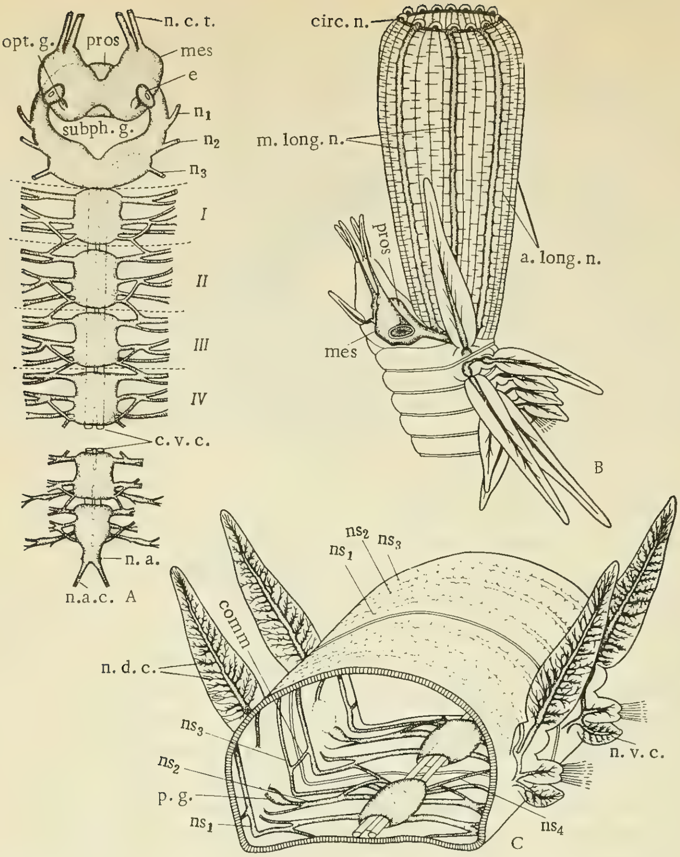

FIGURE 10. Nervous system of Eulalia viridis (after Lebskii, 1970):

A) brain and ventral nerve cord (diagram): e — eye; opt. g. — optic ganglion; c. v. c. — connectives of ventral nerve cord; n_1 — nerve of 1st tentacle segment, n_2 — nerve of 2nd tentacle segment, n_3 — nerve of 3rd tentacle segment; n. a. — nerve to anus; n. a. c. — nerve of anal cirri; n. c. t. — nerve of cephalic tentacle; pros — prosencephalon; subph. g. — subpharyngeal ganglion; mes — mesencephalon; I—IV) neurosomites. B) stomatogastric nervous system (diagram): m. long. n. — main (6) longitudinal nerves; a. long. n. — accessory (18) longitudinal nerves; circ. n. — circular nerve at basal part of terminal papillae. C) relations between segmentary nerves: comm — commissure connecting 1st and 3rd nerve of two adjacent segments; ns_1 — 1st segmentary nerve, ns_2 — 2nd segmentary nerve, ns_3 — 3rd segmentary nerve, ns_4 — 4th segmentary nerve; n. v. c. — nerve plexus in ventral cirrus; n. d. c. — nerve plexus in dorsal cirrus; p. g. — podial ganglion.

established. The nervous system of the Phyllodocidae, described in detail by Pruvot (1885) and Gravier (1896), has been recently described with greater precision by Lebskii (1970). He used the histochemical reaction for cholinesterase, which is specific for the nervous system, and obtained a detailed topographical picture of the nervous system of Eulalia viridis

(Figure 10). According to Lebskii, in addition to the 3 main nerve rings of a segment, there is a fourth, preseptal pair of nerves, which divide near the ventral ganglion and connect the second nerve with the first nerve of the next segment; the third nerve is also connected with the first nerve of the next segment on the lateral surface of the body by a large commissure. This suggests that there is a close connection between the peripheral nervous systems of adjacent segments. Lebskii also established that the subpharyngeal ganglia of E. viridis (Figure 10), which innervate the tentacular cirri of the first 3 segments, have slight constrictions which separate the ganglia into 3 parts, corresponding to the 3 anterior segments. This had been shown partly by Binard and Jeener (1928). According to Pruvot (1885), the subpharyngeal ganglia of Phyllodoce laminosa are pear-shaped and are situated mainly in the 3rd segment. If the above differences in the structure
48 of the subpharyngeal ganglia in Eulalia and Phyllodoce are not due to the methods of examination, they are fundamental and agree with the structure of the anterior segments of these two genera: all 3 anterior segments are distinctly separated in Eulalia, but the 1st segment is reduced on the dorsal side and partly fused with the 2nd segment in Phyllodoce. This indicates that the subpharyngeal ganglion is in an earlier stage of cephalization in Eulalia than in Phyllodoce. In the larval stages of Phyllodocidae (metatrochophore), each larval segment has a separate ganglion of the ventral nerve cord. The degree of external cephalization in adult forms is thus correlated with the structure of the nervous system. However, this has been studied only in a few genera.

The neuronal composition and structure of the neurochord of the Phyllodocidae, including Eulalia, has not been studied, and it is therefore difficult to make a comparison with the Aphroditidae, in which Romm (1960) established markedly differentiated nerve formations in Harmothoe imbricata. According to Erokhina (1968), the brain of the Phyllodocidae (Eteone longa) has a much simpler structure than that of the Aphroditidae (Harmothoe imbricata): corpora pedunculata are absent, differentiation is weak, and the number of nerve cells is much smaller; this is due, according to Erokhina, to the characteristics of the ecology of this species, but it also suggests the greater primitiveness of the Phyllodocidae. The nervous system of polychaetes is discussed in its evolutionary aspect by Bullock and Horridge (1965).

Excretory system. The organs of excretion (nephridia) and the gonads are arranged according to the internal segmentation, metamerically. In the Phyllodocidae, the nephridia are slightly curved, paired ducts, which open on the outside in small nephropores on the ventral side, at the base of the parapodia. Their closed inner part with numerous large cells at the end, solenocytes, passes through the septa and enters the segment before it. Nephridia are absent in the Phyllodocidae only in the anterior segments and in the two or three posterior segments. With the beginning of maturity some complications take place, a broad, ciliated funnel (gonostome), which develops independently of the nephridium, deposits the sexual products on the outside. The structure of the excretory system is the same in different genera of Phyllodocidae (Eulalia, Phyllodoce, Notophyllum); there is only slight variation in the arrangement of the solenocytes (Fage, 1906). A similar excretory system is present in the Alcionidae and Tomopteridae. The Glyceridae and Nephthyidae also have protonephridia with solenocytes, but instead of a ciliated funnel the nephridial duct is connected with a special phagocytic organ. In all other polychaetes (except in the Capitellidae), typical metanephridia are united from the beginning with coelomoducts, and the inner end begins in a constantly functioning open funnel, the nephrostome. The excretory system of all larval forms begins to develop in the form of protonephridia, which suggests that the protonephridia are the most primitive type of excretory system.*

49 Only the intestine of polychaetes has no strictly metameric structure: it is a straight, sometimes undulate tube. However, the intestine of some Aphroditidae also shows indications of metamerism: there are paired lateral blind processes in most segments.

The internal metamerism is absent in the Phyllodocidae only in the anterior part of the body. This is caused by the long and very mobile esophagus, which becomes partly everted to form the proboscis. It is more than half as long as the body in the Phyllodocidae and Glyceridae. Because of the great mobility of the massive pharynx, there is nearly a total reduction of the internal septa in the anterior part of the body, and the coelomic fluid, which is usually isolated in the somites, moves freely throughout the anterior part of the body, which facilitates eversion of the proboscis.

REPRODUCTION AND DEVELOPMENT**

Polychaetes are very labile in their methods of reproduction. Typical for most of them is the free-swimming larval stage, the trochophore, with a complex metamorphosis. The planktonic larval stage is sometimes suppressed and development is direct. Cases of vivipary have been recorded, connected with hermaphroditism and parthenogenesis. Numerous Syllidae and Cirratulidae have asexual reproduction by budding (formation of stolons), with strict alternation of generations.

Only sexual reproduction is known in the Phyllodocidae, Alciopidae, Tomopteridae and Lacydoniidae, and fertilization is always external. In all planktonic polychaetes, the entire cycle of development takes place in the water. Benthic Phyllodocidae have pelagic larvae, but the first stages of embryogenesis develop partly in the benthos. Sometimes, e.g. in Notophyllum, the eggs mature under the dorsal cirri. This method of care for the progeny is most widespread in the Aphroditidae: the eggs develop under the elytra to a free trochophore, but this takes place mainly under unfavorable conditions in the Arctic. Benthic Phyllodocidae usually attach their eggs with mucus to seaweed, pebbles and other objects on the sea bed (Figure 11, *1*). After the eggs have been deposited, the males enter the batch and fertilize them. In these cases, the first stages of development take place under the slimy membrane of the batch, which protects the embryos against unfavorable effects of the environment. The first stages of ontogenesis are very sensitive to slight changes of external factors. Thus, while adult Eulalia viridis in the White Sea, according to Berger and Lebskii

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* Lameere (1925), according to his theory of the origin of the Annelida from the Anthozoa (Cerinatharia), which disagrees with the views of Goodrich (1900) and other authors, considers that the nephromixia are the most archaic type of excretory system of polychaetes, and that the protonephridia developed later; however, it is difficult to accept this.

** Written by V. A. Sveshnikov.

(1969), can tolerate freshening to 6 to 8‰, the trochophores do not tolerate a salinity of 14‰. The impermeable wall of the slime-covered batches reduces the injurious effect of low salinities.

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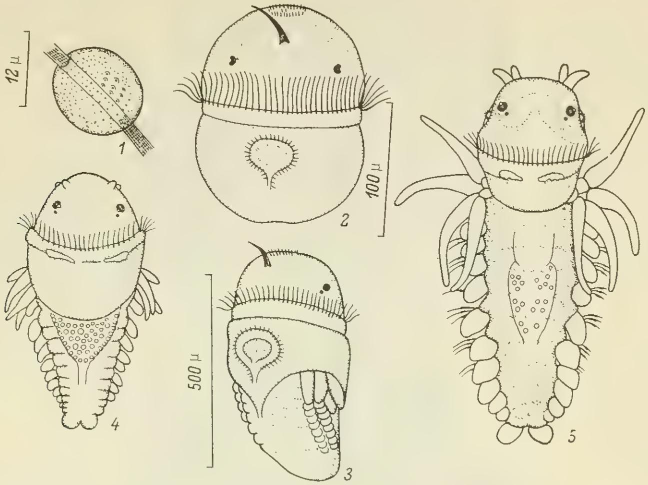

FIGURE 11. Larval stages of *Phyllodoce* (after Sveshnikov):

1) batch of eggs on a leaf of *Zostera*; 2) trochophore; 3) metatrochophore; 4) nectochete; 5) juvenile benthic form.

According to Sveshnikov (1961), embryogenesis in *Phyllodoce* in the White Sea, from fertilization to the hatching of the trochophore, lasts about 6 days. The trochophores lead a free planktonic life and feed on larvae of other invertebrates, rarely on Protozoa and phytoplankton. The trochophores of the Phyllodocidae are monotrochous (with a single ring of cilia). Their speed of movement attains 1.1 mm/sec (Konstantinova, 1969). The trochophore then develops into metatrochophore I, metatrochophore II, and the nectochete. On attaining a certain size, the nectochete descends and settles on the bottom.

A high fertility is characteristic for many Phyllodocidae: a single batch may contain over 150,000 eggs (Petrovskaya, 1960), and several thousand larvae are sometimes found in 1 m^3 in the plankton. Unfavorable conditions of temperature and salinity in the spawning period may sharply reduce the numbers of larvae. The pelagic larvae of benthic Phyllodocidae serve for dispersal and spread over large distances.

The first data on the development of larvae of Phyllodocidae were given by Agassiz (1867) and McIntosh (1869), who described the metatrochophore and nectochete of *Phyllodoce maculata* from the coasts of the North Atlantic Ocean. The development of *Lopodorhynchus* was studied in detail at the end of the 19th century (Kleinenberg, 1886; Meier, 1897); these data were amplified by Åkesson (1967). Some observations on reproduction and development were made by Gravier (1923). The development of
51 *Eulalia viridis* was described by Meyer (1938). Thorson (1946) gave a comprehensive review of the literature and his observations on the larval forms of several species of Phyllodocidae. The larvae of *Phyllodoce tuberculata* from the Black Sea were described by Kiseleva (1957a) and those of

Ph. maculata from the Barents Sea by Petrovskaya (1960). Some Phyllodocidae from the White Sea and Sea of Japan have been recently studied by Sveshnikov (1961, 1967). The embryology and larval development of Tomopteris helgolandica have been studied by Åkesson (Åkesson, 1962; Åkesson and Melander, 1967). The larval development of the Lacydoniidae was first observed by Bhaud (1967). Details on the development of the Alciopidae have not been published so far. There is only information on Alciopina parasitica (Claparède and Panceri, 1867; Granata, 1911). The postembryonic development of some Phyllodocidae has been studied in greater detail than that of other families.

The trochophores, metatrochophores, and sometimes the nectochetes of benthic Phyllodocidae have one character in common: an eccentric ring of cilia (rarely two rings, symmetrically arranged), which is displaced from the animal pole toward the mouth (Figure 11). According to this character, the larvae of Phyllodocidae belong to the type of "cirraria" (Sveshnikov, 1963).

(52)

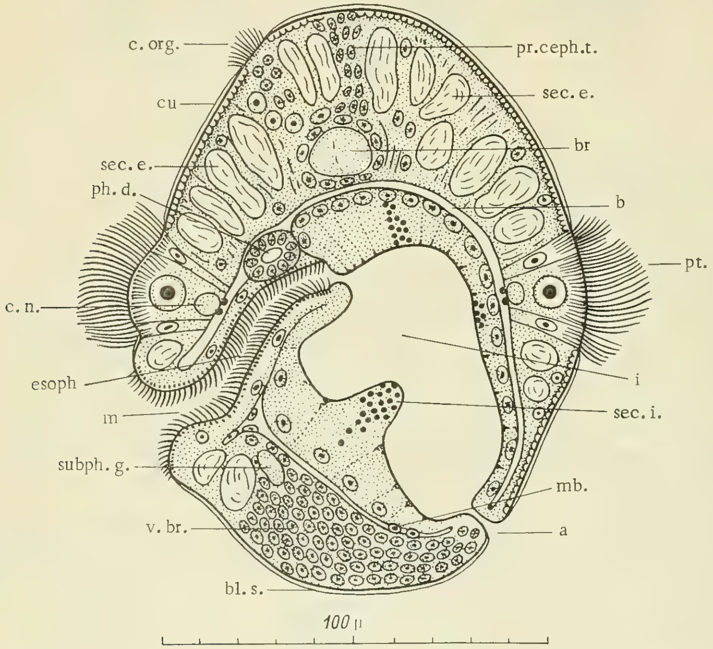

FIGURE 12. Trochophore of Phyllodoce maculata, sagittal section (after Sveshnikov):

a — anus; b — blastocoel; bl. s. — surface of blastopore; v. br. — primordium of ventral brain; ph. d. — diverticulum of pharynx; pr. ceph. t. — primordium of cephalic tentacle; i — intestine; cu — cuticle; c. n. — circular nerve; br — brain; c. org. — ciliary organ; mb. — mesoblast; esoph — esophagus; subph. g. — subpharyngeal ganglion; pt. — prototroch; m — mouth; sec. i. — secretory cells of intestine; sec. e. — secretory cells of epithelium.

The pigmentation of the trochophores of the Phyllodocidae varies, but it is mainly green, yellow or orange. Some trochophores have on the episphere,

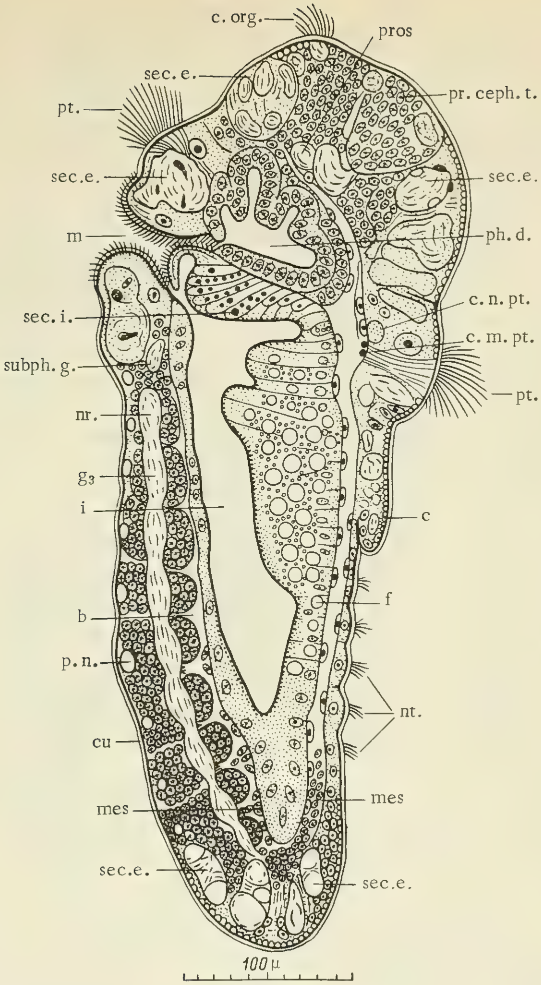

FIGURE 13. Metatrochophore of Phyllodoce maculata, sagittal section (after Sveshnikov):

b — blastocoel; c — collar; g_3 — ganglion of 3rd segment; ph. d. — diverticulum of pharynx; f — droplets of fat; pr. ceph. t. — primordium of cephalic tentacle; i — intestine; cu — cuticle; c. m. pt. — circular muscle of prototroch; c. n. pt. — circular nerve of prototroch; c. org. — ciliary organ; mes — mesenchyme; nr. — neuropile; nt. — nototroch; subph. g. — subpharyngeal ganglion; pros — prosencephalon; p. n. — parapodial nerves; pt. — prototroch; m — mouth; sec. i. — secretory cells of intestine; sec. e. — secretory cells of epithelium.

and metatrochophores on the prostomium, a "collar" (Figure 13, c) and on the pygidium large, paired lemon-yellow spots which reflect incident light. Tactile sense organs and probably chemoreceptors are represented by a pair of rings, or a single tuft of cilia, in the apical area. The eyes are usually red, with or without a lens. The body of the trochophore and metatrochophore is divided by an equatorial girdle of cilia, the prototroch. It consists of large cells arranged in three rows (Figure 12, pt.). The middle row contains the largest cells and cilia. The equatorial girdle is accompanied by a neuromuscular ring (Figure 12, c.n.), crossed by 5–7 pairs of meridional neuromuscular cords. This number is different in the upper and lower hemisphere. There are 11–15 such cords in the episphere. A single cord passes on the ventral side, and the other neuromuscular cords are arranged symmetrically in pairs. All cords become branched near the animal pole. The single neuromuscular cord divides in the lower hemisphere and surrounds the mouth. A pair of dorsal muscle cords in the lower hemisphere surrounds the anus. The trochophore may also have 2 or 3 complete or incomplete rings in the upper, and one ring in the lower hemisphere. These rings are situated parallel to the equator. Differentiation of cells takes place in the ectoderm of the animal pole and the primordium of the brain is formed (Figure 12, br); the primordium of the ventral nerve cord is formed at the vegetative pole (Figure 12, v.br., subph.g.).

The epithelium of the trochophore and metatrochore consists of cutaneous and mucus-secreting cells (Figure 12, sec.e.). Near the mouth area there are some large, ciliate, eccentrically situated cells of the parietal organ (Figures 12, 13, c.org.).

A large part of the trochophore is occupied by the intestine. The oral area is transformed into a narrow esophageal tube, which consists of cells with strong cilia (Figure 12, esoph). The esophagus contains circular and
52 longitudinal muscle fibers. The wide part of the intestine (i) consists of two chambers, connected by a slit (sec.i.). Both chambers have a ciliate lining. The posterior chamber opens to the outside through the anus, which is situated in the center of the hyposphere. There are numerous yolk granules in the walls of the intestine. The paired primordium of the pharynx is formed in the trochophore (ph.d.).

The stage of the metatrochophore begins with the appearance of segmentation. The number of segments is relatively large. There are 7 segments in larvae of Eteone (Figure 14). The oral segment bears no setigerous follicles. After formation of the larval segments, there is usually an interval in which no new postlarval segments are formed. The metatrochophore and nectochete pass through marked morphological changes, but the number of segments remains constant.

The metatrochophore of Phyllodoce has a glandular collar surrounding the oral segment (Figures 11, *3*; 13, c). Segmentation of the metatrochophore develops first in the ectoderm, extending later to the mesoderm.
54 In the metatrochophore of Phyllodoce (Figure 13), which has 11 segments, segmentation in the ectoderm is indicated by dorsal ciliary half rings, the nototrochs (nt.), the ventral nerve cord ganglia (subph.g. and g), the setigerous follicles and the nerves of the parapodia (p.n.). The blastocoel is not segmented at this stage (b) and mesenchymal cells (mes) are freely distributed in it from the anus to the animal pole. In some larvae, septa and mesenteries may be formed schizocoelically, and in the postlarval body
55 teloblastically. Schizocoelic processes of metamerism of the larval coelom have been observed in Eteone longa.

In the nectochete, the parapodia of the larval part have become mobile, and setae grow from the setigerous follicles which assist floating in the water. The larva has at this stage the habitus of the adult animal and is ready to settle on the bottom. However, provisional systems of organs still retain their importance in most larvae, and the nectochete is able to lead a

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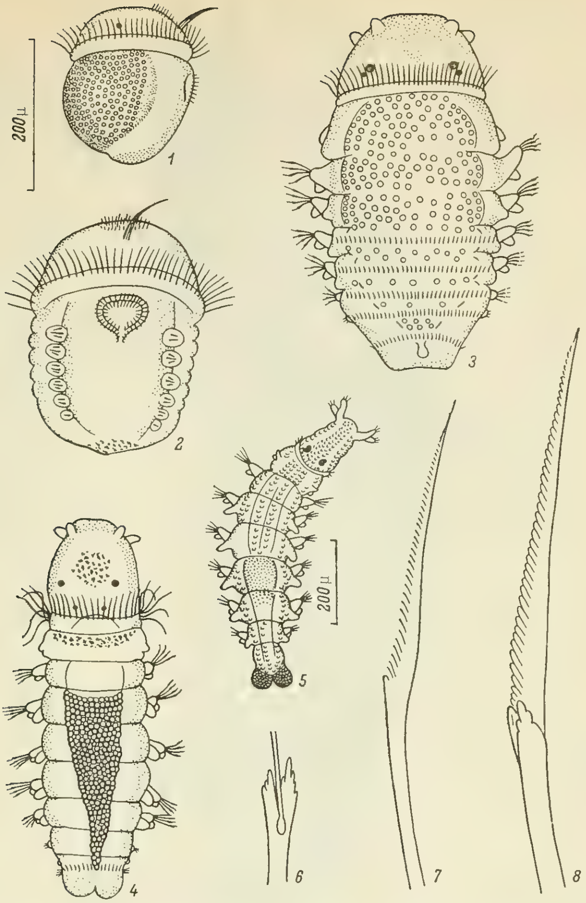

FIGURE 14. Larval stages of Eteone longa (after Sveshnikov):

1) trochophore; 2) metatrochophore; 3) early nectochete; 4) late nectochete; 5) benthic juvenile semisegmented form; 6—8) complex and simple setae of juvenile form.

pelagic life. Thus, complete ciliary rings and dorsal half rings are preserved in some nectochetes of Eteone longa (Figures 14; 15, pt.,tt., nt.), as well as the orthogonal neuromuscular ring (c.n.pt.) and, to some extent, the blastocoel and other provisional adaptations. At the same time, all adaptations necessary for benthic life, like the oligomerous semisegmented body which can bend with the aid of the seta-bearing parapodia, are already developed in the nectochetes of Eteone longa. The definitive nervous system is fully developed and functional. The brain is divided into regions and each region is differentiated (g.ceph.t.); normal ganglionic and giant neurons are present (n.neur.). Near the prosencephalon and mesencephalon of the nectochete are a single and two paired coelomic cavities (coel). In the adult Eteone longa the brain is surrounded by a single and four paired coelom-
56 ic cavities (Erokhina, 1968). The ventral brain is divided into 7 ganglia,

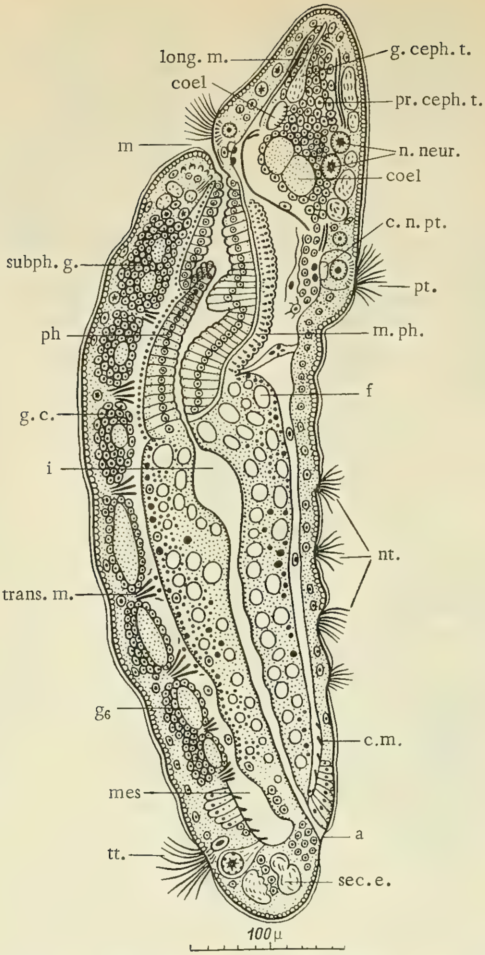

FIGURE 15. Nectochete of Eteone longa, sagittal section (after Sveshnikov):

a — anus; g. ceph. t. — ganglion of cephalic tentacle; g_6 — ganglion of 6th segment; g. c. — ganglion cells of ventral brain; ph. — pharynx; f — droplets of fat; pr. ceph. t. — primordium of cephalic tentacle; i — intestine; c. m. — circular muscles; c. n. pt. — circular nerve of prototroch; mes — mesenchyme; m. ph. — muscles of pharynx; nt. — nototrochs; subph. g. — subpharyngeal ganglion; long. m. — longitudinal muscles; pt. — prototroch; m — mouth; trans. m. — transverse muscles; tt. — telotroch; coel — coelom; n. neur. — nuclei of giant neurons; sec. e. — secretory cells of epithelium.

corresponding to the number of larval segments (subph.g.–g_6). The definitive musculature of the larva consists of circular, longitudinal and transverse cords (c.m., long.m., trans.m.). The pharynx (ph) is formed, but still has a weak musculature (m.ph.) and cannot be everted. It appears, therefore, that in the nectochete the definitive systems are developed better than the provisional systems, and the organism, which lives at this stage in water, is completely adapted to a benthic life.

Transition to life at the bottom is accompanied by numerous attempted descents and returns to the surface in search of a favorable place. In larvae of Eulalia and Phyllodoce, these attempted descents are particularly numerous and the search prolonged. Larvae which have settled on the bottom therefore often have a large number of segments (Figure 11, 5). The juvenile forms live for some time in a "web," and then go over to a free-living mode of life.

There is no great difference between the development and structure of the trochophores, metatrochophores and nectochetes of benthic Phyllodocidae and the pelagic Lopadorhynchus. The provisional systems of organs of the trochophores of Phyllodoce and Lopadorhynchus are identical. The parietal organ of larvae of both genera begins to develop as a paired formation, however, it develops later mainly on the right side. The systems of the provisional ectodermal muscles and of the orthogonal nervous system are very similar in both genera. The definitive systems, particularly the nervous and muscular systems, develop similarly in Lopadorhynchus, Phyllodoce and Eteone. The brain develops as a paired formation near the animal pole. The primordium of the ventral brain is also paired. In the trochophores of Lopadorhynchus, the surface of the blastopore is thickened and situated at a right angle to the main axis of the larva. This is also the case with the trochophore of Phyllodoce (Figure 12, bl.s.). Setigerous follicles are formed in the ectoderm on this surface and are accompanied by nerves and muscular cords of the parapodia. The paired longitudinal ventral and dorsal muscle cords develop before the others. The tangential and parapodial muscles develop later.

There are also only minor differences in these genera in the formation of the paired pharyngeal diverticula and of the pharynx. The paired diverticula of the pharynx develop as blind pockets of the stomodeum, or of the esophagus. The paired diverticula of the pharynx of the larvae of Phyllodocidae strongly resemble in situation and morphology those of some Archiannelida, e.g. Dinophilus (Shimkevich, 1895) and Polygordius (Zalenskii, 1907).

The postembryonic development of the Tomopteridae was studied by Åkesson (1962). The trochophore of Tomopteris helgolandica hatches 30—40 hours after fertilization. This trochophore has only little embryonic tissue in the episphere. This is different in many trochophores of the Phyllodocidae and other polychaetes. The trochophores of Tomopteris apparently do not belong to the "cirraria" type (Sveshnikov, 1963). The parietal ring of cilia is absent in the trochophore of Tomopteris, as there are no groups of cells at the animal pole which correspond to the primordium of the brain. There is instead an invagination on the episphere, slightly above
57 the line of the trochoblasts and near the equator, a paired primordium of the brain from which the brain, chemoreceptors and photoreceptors (Figure 16, A, B, cer.invag.) develop later. In the hyposphere develops another paired primordium (s.pl.), also by invagination, from which later develop the somatic plate, the ventral nerve cord and the parapodia with developing setae; the mesoblasts develop into the musculature and coelomic lining. Invagination during the development of the nervous system of Tomopteris may be considered as a primitive character, indicating the great age of the family Tomopteridae. The development of the nervous system and sense organs, both in the larvae and adults of Tomopteridae, is slight. This may be connected with the weak mobility and activity of the Tomopteridae, although cases of feeding on fish fry and arrow worms are known (pp. 26, 27).

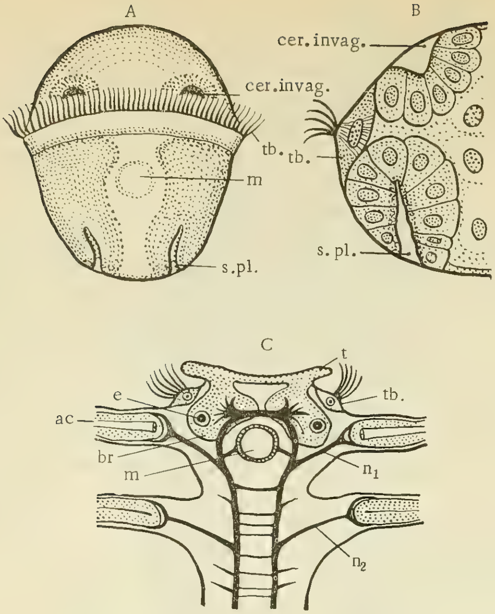

FIGURE 16. Postembryonic development of Tomopteris helgolandica (after Åkesson, 1962):

A) trochophore, 30 hours old; B) section through trochophore, 32 hours old; C) diagram of the organization of the nervous system in a larva 6 days old: ac – aciculum; e – eyes; br – brain; n_1 and n_2 – nerves of 1st and 2nd segment; m – mouth; s.pl. – invagination, forming somatic plate with ventral nerve cord, segments and mesoderm; t – tentacles; tb. – trochoblasts; cer.invag. – cerebral invagination.

The presence of primary heteronomous metamerism has been proved for Tomopteris helgolandica. Five larval segments are gradually formed at first. The 4 anterior segments develop more rapidly than the 5th. The 2nd segment develops at first more rapidly than the 1st and 3rd, but the 1st segment, with a thick axial aciculum, develops more rapidly than the 2nd.
58 After the 5th and 6th segments have begun to develop, there is an interval of several days, and then the postlarval segments begin to grow.

The postembryonic development of the Typhoscolecidae, which was unknown until now, is of special interest. A description of the larva of Typhloscolex muelleri, which has 7 segments according to Sveshnikov, is given below (Figure 17). This larva corresponds to the metatrochophore. The main characters of its organization are as follows: weak development of the central nervous system and a specialized apparatus for obtaining food. The strong development of the mesenchyme, which later forms a kind of parenchymatous tissue in the larval and postlarval parts, is characteristic. This may be considered both as a primitive and as a secondary character.

The cephalic end of the larva of T. muelleri is thickened and bears the prototroch (Figure 17, pt.). In the center of the animal pole is situated a single tentacle covered with short cilia. A large area of the animal pole is

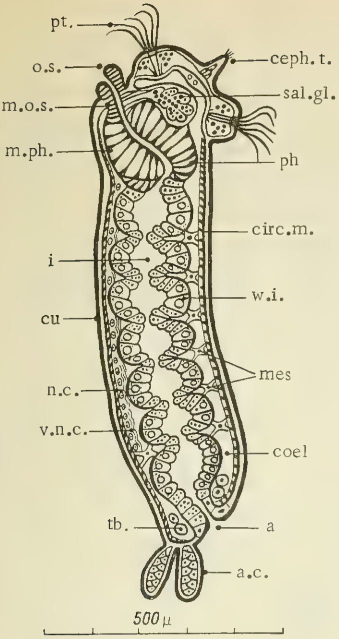

FIGURE 17. Structure of the larva of Typhloscolex muelleri with 7 segments. Sagittal section (after Sveshnikov):

a – anus; a.c. – anal cirri; v.n.c. – ventral nerve cord; ph – pharynx; ceph.t. – cephalic tentacles; i – intestine; cu – cuticle; circ.m. – circular muscles; m.ph. – muscles of pharynx; m.o.s. – muscles of oral sucker; mes – mesenchyme; n.c. – nerve cells; coel – body cavity; pt. – prototroch; o.s. – oral sucker; sal.gl. – salivary glands; w.i. – wall of intestine; tb. – trochoblasts.

occupied by trochoblasts (tb.), while elements of the nervous system occupy only a small part of the epithelium. This character of the larva (and of the adult) suggests a relatively passive mode of life. The weak development and differentiation of the nervous system, and the absence of eyes are evidence of this.

The second distinctive character of the larva is the structure of the apparatus for seizing food, the circumoral lips and the pharynx with salivary glands. The morphology of this apparatus shows that it cannot be everted as in predacious polychaetes (Dales, 1962). The pharynx of T. muelleri is a typical swallowing apparatus of the pumping type. The pharynx is strongly swollen, almost spherical. The muscle cords are arranged radially some distance from each other, which suggests that the volume of the pharynx can be changed considerably (ph). The circumoral lips also have a strong musculature and are extended upward like a tube. At the base of the lips, on the dorsal side, opens the salivary duct (sal.gl.). Behind the
59 pharynx is the intestine, with deep constrictions in each segment, so that the intestine seems to be divided into 7 chambers. The cells in the walls of the chamber form groups of gland cells mainly between the chambers, while groups of cells which absorb food are situated in the more central parts of the chamber. Such an alternating arrangement of the epithelial cells forms differentiated parts for digestion and absorption of food (i). A similar arrangement is common also in other polychaetes. But in T. muelleri, the structure of the intestine shows distinctly primitive characters, possibly related to its semiliquid food. According to the structure of the mouth and pharynx, T. muelleri is probably ectoparasitic, feeding on pelagic Coelenterata (siphonophores, medusae, tenophora). Typhloscolex probably maintains a vertical position in the water. Movement of strongly developed

cilia of the prototroch causes a vertical movement upward. When the apical tentacle touches the surface, the activity of the prototroch ceases and the animal sinks slowly. After descending to some depth, the action of the prototroch begins again and the animal rises to the surface. This type of behavior is typical for the veliger larvae of molluscs and other pelagic organisms, e.g. the tentaculate Ctenophora. If Typhloscolex rises to the surface, it may find a medusa or siphonophore. The lips, directed upward like a tube, attach themselves to the prey by sucking movements of the pharynx. The salivary glands secrete a digestive fluid which dissolves the integument of the prey. Further sucking movements cause the semiliquid tissues to be swallowed. Feeding on small planktonic organisms is unlikely with this structure of the pharynx.

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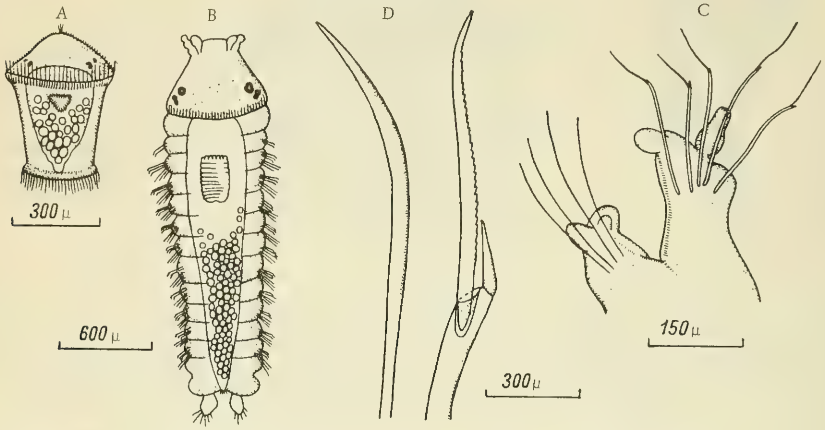

FIGURE 18. Larval stages of Paralacydonia paradoxa (after Bhaud, 1967):

A) early trochophore; B) nectochete; C) parapodia; D) simple dorsal and complex ventral seta.

There are distinctly primitive characters in the organization of the Typhloscolecidae, mainly the retention of provisional systems, like the prototroch, in adults. There are also some special characters in the structure of the cutaneous-muscular sac. The transverse section is often square or rectangular; the main development takes place at first in 4, later in 6, longitudinal muscle cords; the muscles of the parapodia are weakly developed. The leaf-shaped appendages have no special musculature and are apparently little mobile; they only increase the surface of the body and assist floating in the water.

The larval development of the Lacydoniidae has become known only recently (Bhaud, 1967). The early trochophore of Paralacydonia paradoxa has two ciliated rings, the prototroch and the teletroch, which closely resemble the trochophore of Nephthys. However, it has a bundle of apical cilia, which is characteristic for the Phyllodocidae. The nectochete, which settles on the bottom, has 11 setigerous segments behind the prototroch (Figure 18); chitinous jaws are absent. Paralacydonia thus seems to have characters typical for both the Nephthyidae and the Phyllodocidae.

The above shows that the larvae of the Phyllodocidae, Tomopteridae and Typhloscolecidae of the suborder Phyllodociformia are different. This is

60 typical for groups with primitive characters. The higher groups, which have attained a definitive form, show a relatively greater uniformity of structure in the larvae and adults. It is characteristic that cephalization in all larval forms of the Phyllodociformia remains at a low level. It has to be stressed that metamorphosis of the larvae of the Phyllodociformia is always evolutionary, without any indication of necrotic metamorphosis, which is present in the Amphinomidae and Oweniidae.

ECOLOGY

The Polychaeta are generally extremely eurybiontic, but many species have a very narrow ecological specialization. The families dealt with in this work do not form a special ecological group. The family Phyllodocidae contains mainly benthic forms, but also some pelagic species. The adults of the very small family Lacydoniidae lead a benthic mode of life. The other three families — Alciopidae, Tomopteridae and Typhloscolecidae — are holoplanktonic and pass their entire life in the water.

Most Polychaeta are typical marine animals, and are the dominant forms of the benthos. There is in fact no biocenosis in which some polychaetes do not have an important role.

Their ecological plasticity is very high. In addition to the marine forms, many species of Polychaeta inhabit brackish water, particularly estuaries of tropical rivers (e.g. the Nereidae). There are also freshwater species, in continental inland water bodies; for instance, Manayunkia baicalensis occurs in the lakes Taymyr and Baikal and in the Angara River, and Marifugia cavatica inhabits subterranean rivers and lakes in Yugoslavia; 61 these two species belong to highly specialized families: M. baicalensis to the Sabellidae, and M. cavatica to the Serpulidae.

Altogether, 130 species live in brackish and fresh water (Wesenberg-Lund, 1958), and of these 43 species have been recorded in continental freshwater bodies. Brackish-water and freshwater species constitute less than 2% of all known species of polychaetes (over 6000). There is not a single family which inhabits exclusively brackish water; this suggests that the polychaetes spread into fresh water bodies relatively recently. In the freshwater areas of the Polar basin and the seas of the Northwest Pacific (coastal lagoons, river estuaries) about 20 species have been found which inhabit brackish water; they belong to 6 marine families (Okuda, 1935; Ushakov, 1948b; Rullier, 1957; Klyuchereva et al., 1964; Tang Ngok T'han, 1967). The Phyllodocidae are not mentioned by Wesenberg-Lund or in any other work on the fauna of brackish water. However, the ability to tolerate temporary freshening for some time is relatively strong in some Phyllodocidae. This is mainly characteristic for species inhabiting the zone subject to ebb and tide (Eulalia viridis, Phyllodoce maculata), which frequently find themselves in conditions of strong freshening of the water when it recedes. The profuse mucus apparently serves as a protective adaptation in these conditions. Wu Pao-ling and Chen Mu (1963) only recently found Eteone in the Yangtse River near Shanghai, where low salinities are prevalent; they described it as a new species E. delta (p. 167). Volova (1969) recently found in distinctly fresh coastal lakes in the Southern Maritime Territory a small Eteone which resembles E. longa and inhabits the lakes together with the typical brackish-water species Nereis japonica and Prionospio japonicus. There are no other records of Phyllodocidae from fresh or markedly freshened water. It is interesting that some Nereidae (Lycastis, Lycastopsis and Nereis) have become adapted in the tropics (Sumatra, Philippines) to a true terrestrial, amphibiotic mode of life and live in damp soil among the roots and bark of palms and banana leaves, distinctly above sea level, 25 miles from water (Pflugfelder, 1933; Berkeley and Berkeley, 1963).

Numerous polychaetes (Capitella capitata and others) tolerate strong pollution of seawater and can live in almost anaerobic conditions (Yakubova and Mal'm, 1930; Bellan, 1967, 1968; Bellan-Santini, 1968). The Phyllodocidae are apparently more sensitive in this respect and have not yet been found in strongly polluted biotopes.*

A very rich and diversified fauna of Polychaeta has been observed on the sea shelf, particularly at low latitudes. Species inhabiting zones which are subject to drainage are adapted to very changeable and often unfavorable conditions. Some littoral forms of the northern seas of the USSR show an exceptional resistance to frost. Thus, in Eastern Murmansk, in marine baths in the supralittoral zone and in the zone subject to drainage, Eulalia
62 viridis tolerates in winter temporary cooling to −3°C (Zhyubikas, 1969), and according to Khlebovich (1957), adult littoral Eteone longa on the Kuril Islands regained normal locomotor reactions under experimental conditions after freezing for 3 days to −4°C. The degree of cold-resistance of different species of polychaetes is to some extent correlated with the conditions in which the worms live. According to Polyanskii's experiments (1950) in Murmansk, Spirorbis borealis, which lives on fucus in the zone subject to drainage and becomes exposed during recession of the water to very low temperatures in winter, is much more cold-resistant than Sp. spirillum, which lives in the sublittoral zone and is therefore not subjected to extreme cold. Sp. borealis tolerates temperatures of −12° and −14° for 3 days under experimental conditions, and only temperatures of −18° and 20° prove lethal after several hours; on the other hand, freezing of Sp. spirillum to −5° and −7° kills it rapidly. Unfavorable external conditions adversely affect mainly the larval forms (p. 42).

Many species of polychaetes often form large colonies. The following data show how dense some colonies are: near the western coast of Kamchatka their biomass may attain 272 g per m^2 (Gordeeva, 1948), and in the Bering Sea (Anadyr Bay) 220 g per m^2; the main mass in this case is formed by Maldane sarsi, to 2000 specimens per m^2 (Levenshtein, 1960). There may be 90,000 specimens per m^2 in the Barents Sea (Sveshnikov, 1968). In the Baltic Sea, Pygospio elegans forms colonies of to 100,000 specimens per m^2 (Arndt, 1964). In the tide zone of the Shantar Islands in the Sea of Okhotsk, colonies of Oridia rivalaris (Sabellidae) have a density of to 40,000 specimens per m^2 (Zaks, 1929) and in Murmansk, specimens of Fabricia sabella may number to 167,000 per m^2 (Matveeva et al., 1955).

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* In oil refineries, in which seawater is used for refrigeration to control biological growths, chlorine is added to seawater, and the pH is markedly lowered. Zibrovius and Bellan (Tethys, Vol. No. 2, 1969, pp. 375–382) report that in these cases, growths of Mytilus and Ostrea were exterminated, but large numbers of Serpulidae developed (Pomatoceros triqueter), and many other polychaetes, including Eulalia viridis, were not affected.

Such large colonies are never formed by Phyllodocidae, although in the littoral and on the upper horizons of the sublittoral zone of Murmansk and of the White Sea during the spawning period Eulalia viridis and Phyllodocide maculata often form dense groups. In the coastal biocenoses of Pos'et Bay in the Sea of Japan, according to Buzhinskaya (1967), the numbers of Phyllodocidae may be as follows (per m^2): small Phyllodoce to 50, Eteone longa to 50, Eulalia viridis to 20 specimens.

The distribution of Polychaeta extends to a depth of 10,000 m. Below 2000 m the species become less numerous. Thus, in the Pacific Ocean, at a depth of 2000–3000 m the number of species was 109; at 3000–4000 m 67; at 4000–5000 m 56; at 5000–6000 m 16; at 6000–7000 m 19; at 7000–8000 m 14; at 8000–9000 m 17; and below 9000 m 9 species (Levenshtein, 63 1969).* At the same time, according to dragging of the bottom, the relative role of polychaetes increases with depth. Thus, according to Levenshtein (1960), polychaetes constitute only about 6% of the total benthic biomass in the Bering Sea between 0 and 100 m, but to 50% between 3000 and 5000 m; similar figures are given by Kuznetsov (1963, p. 60) for the southern Kamchatka area and by Belyaev and Ushakov (1957) for the Antarctic.

The fauna of Polychaeta of abyssal waters is very specific. Especially characteristic are numerous species of Aphroditidae of the genera Macellicephaloides and Macillicephala (Ushakov, 1955b). Most species of Phyllodocidae so far found at large depths are specific for abyssal waters. The genera Vitiazia (p. 157) and Vitiaziphyllum (p. 158) have been recorded at great depths in the Pacific. However, numerous genera of Phyllodocidae, particularly the more primitive genera, have a very wide bathymetric range; thus, species of Lugia, Mystides, Protomystides and Eteone have been found at depths from 0 to almost 6000 m. Typical characters of abyssal Phyllodocidae are as follows: disappearance of the eyes, weak pigmentation and very long setae, which probably facilitate movement over soft ground. Some abyssal Phyllodocidae, e.g. Vitiazia dogieli (p. 157), show a wide variation of the podial appendages, which suggests that the systematic characters have not become definitively established in abyssal species because of their relatively recent appearance in very deep water (Vitiazia dogieli was found at depths between 6157 and 8100 m).

Most Polychaeta are benthic animals, but during the beginning of maturity some of them (Nereidae, Syllidae, Eunicidae and some benthic Phyllodocidae) undergo morphological adaptations, natatorial setae, very long podial appendages, etc., and rise to the surface, where they lead a temporary pelagic mode of life, which ensures the meeting of males and females. These forms are named epitokous forms. The morphological modifications of the Nereidae during epitoky have been mentioned above in the description of the parapodial complex (p. 30). In the Syllidae and Eunicidae, such modifications are much more far-reaching than in the Nereidae. Autolytus (Syllidae) comes to the surface with a markedly modified cephalic end and distinct sexual dimorphism, so that pelagic males, with large double palps, were at first considered to belong to an independent genus *Polybostrichus*, and pelagic females of *Autolytus*, without palps and with large pockets on the ventral side, in which the eggs are carried after deposition, were described as the independent genus *SaccONereis*. The palolo of the Pacific Ocean (*Eunice viridis*), which lives in coral reefs in Fiji and Samoa, does not come to the surface complete when its genital products become mature; only its posterior parts, filled with the genital products, rise to the surface, while the anterior parts (atokous parts) remain at the bottom and regenerate the posterior parts. The Atlantic palolo (*E. fucata*), which inhabits the sea near the Antilles, behaves similarly.

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* These data are probably not complete because of insufficient study of the abyssal fauna. Hessler and Sanders (1967) used an "epibenthic trawl" of new construction for the examination of the fauna of the bottom at great depths. In a single trawling they obtained in the Atlantic Ocean: at a depth of 1400 m 10,765 polychaetes of 89 species, and at a depth of 2500–4700 m 305–720 specimens of 43–58 species. These data do not permit evaluation of the density per m^2, but they give evidence of the great diversity of species constituting the bathyal and abyssal fauna.

During epitoky, so-called "swarming," or "epigamic dances," are observed on the surface at night, often coinciding with some lunar phases 64 (Kiseleva, 1957b; Khauenshil'd, 1964; Cazaux and Labourg, 1967). It is easy to collect the worms at these times by attracting them to light, with an ordinary lamp or with an underwater source of light (Gravier and Dantan, 1936). A "lunar periodicity" has been observed in *Eulalia punctifera* near the Atlantic coast of France (Fage and Legendre, 1926). Epitokous forms which rise to the surface are formed also by *Eteone longa* (Rasmussen, 1956). However, the Phyllodocidae never show such sharp morphological modifications as the Nereidae, Syllidae and Eunicidae; the modifications during epitoky are restricted mainly to the appearance of additional long, hairlike setae, which facilitate drifting in the water. Epitoky in the Phyllodocidae is at its earliest stages.

There are species of polychaetes which live in a permanent state of suspension (holoplanktonic), e.g. the families Alciopidae, Tomopteridae and Typhloscolecidae, and some species of Phyllodocidae. Some Aphroditidae are facultatively planktonic.* Most planktonic polychaetes are bathypelagic. All of them are well adapted to life in the water (drifting) and show in this respect characters of convergence with other pelagic invertebrates, particularly with pelagic Nemertini and Chaetognatha. For example, the "whiskers" of *Tomopteris* resemble to some extent those of *Nectonemertes* (which possibly have the same function as the antennae of the Copepoda); the anal cirri of *Travisiopsis* resemble the caudal fin of *Sagitta*. These appendages are steering devices. There are some functional convergent resemblances between the parapodial fins of *Tomopteris* and the fins of pelagic Heteropoda and Pteropoda, but these formations are quite different morphologically. The adaptations of the parapodia of pelagic polychaetes have been discussed above (p. 31). An additional adaptation to drifting is the abundance of fat inclusions, e.g. in *Pelagobia* and *Phalacrophorus* (Friedrich, 1949). Many pelagic polychaetes are completely transparent, which is characteristic for most free-swimming pelagic animals, so that they are almost invisible in the water. However, *Sagitella*, which inhabits great depths, is bright crimson (Southern, 1910a). This has also been observed in abyssal pelagic Nemertini.

It is characteristic for the Phyllodocidae that there are both benthic and pelagic forms among its species, and this eurybiontic character again emphasizes the primitiveness of the family. All other families of Polychaeta are adapted, more or less, to definite conditions of habitat. The question 65 whether pelagic or benthic forms are the original forms in the Phyllodocidae is discussed below (p. 68).

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* The following Aphroditidae have been found in plankton: *Nectochaeta grimaldi* (? = *Quetieria pelagica*), *Drieschia pelagica* and *Podarmus ploa* (= *P. atlanticus*), which are possibly delayed postlarval stages of *Lepidasthenia*. Some adult benthic Aphroditidae, e.g. *Antionoella sarsi* (Arndt, 1964), may also remain suspended in the water at certain periods.

All benthic Phyllodocidae are free-living and live in the benthic littoral vegetation, in colonies of Cirripedia and bivalve molluscs and on mixed ground, with pebbles, gravel and broken rocks with an admixture of silt. They use natural hollows in the ground as shelters, but some burrow deep into sand or sandy silt (Eteone). The Phyllodocidae do not build permanent galleries or tubes in the ground, but construct only temporary mucous habitations. The benthic Phyllodocidae do not show any morphological or ecological specialization.

PARASITISM AND PARASITES

Parasitism is relatively rare among the polychaetes. Most cases of parasitism have been recorded in the Eunicidae (Clark, 1956; Pettibone, 1957). Polychaetes parasitize mainly in the body cavity of other polychaetes (Syllidae, Spionidae, Terebellidae, Serpulidae), rarely in Echiurida. An instance of ectoparasitism is the small Ichthyotomus sanguinarius, which attaches itself with two stylets which form a kind of scissors to the fins of eels and suck their blood.

No parasitic forms have been developed in the benthic Phyllodocidae, but they enter empty tubes of polychaetes; this may be considered as the first stage of commensalism, which is common in the Aphroditidae. A peculiar instance of parasitism has been observed in some species of Alciopidae: juvenile stages of Alciopina parasitica spend part of their life cycle in Cydippe (Claparède and Panceri, 1867). The same Alcionidae have been found in the branchial cavity of the giant Japanese spider crab Macrocheira kaempferi (Paris, 1956). Typhloscolex muelleri, according to Reibisch (1895), possibly sucks the blood of Appendicularia, and according to Sveshnikov (p. 61), of Scyphomedusae and other large pelagic Coelenterata, using an organ resembling a retorte which acts like a sucker. It is not always easy to distinguish between parasitism and commensalism. Coexistence of various Aphroditidae with Echinodermata is usually one-sided and distinctly more advantageous for the worms.

Polychaetes are often the hosts of ecto- and endoparasites; some specificity of the parasites has been observed, and further study of the parasites of polychaetes may provide an additional character for the separation of related species. A large number of commensals and parasites, Infusoria, particularly Suctoria, colonial and solitary Kamptozoa, parasitic Copepoda and others live on Aphroditidae. Many parasites live in the Phyllodocidae. Rhopalura pterocirri has been found in the body cavity of Pterocirrus macroceros (Gravier, 1896). Copepoda of the family Phyllocolidae parasitize on Phyllodoce and Eulalia (Laubier, 1961). Infusoria of the 66 order Peritricha settle on the parapodia and dorsal cirri of Phyllodocidae. According to Yankovskii, Vorticella and species of Intranstyllum and Scyphidia have been found on Phyllodoce maculata from the Kuril Islands and Southern Sakhalin. In the coelomic cavity of Eulalia viridis from the Mediterranean cysts have been found of Haplosporidium (Théodorides and Laubier, 1964), and in E. viridis from the White

Sea, the parasitic nematode Contracaecum aduncum (Buzhinskaya and Lebskii, 1971).

A very characteristic and peculiar instance of parasitism are larval stages of Cunina lativentris (Narcomedusae), which parasitize in the body cavity of Tomopteris nisseni (Damas, 1936); the presence of the embryonic stages of the Narkomedusae causes castration of the host.

PRINCIPLES OF CLASSIFICATION

Main characters of primitive structure and biology of polychaetes

The predacious and free-living mode of life of the ancestral polychaetes was apparently the original mode of life of all recent Polychaeta. Further evolution proceeded by adaptive radiation. The pressure of predators resulted in the development of the capacity to burrow into the ground and to build shelters in the form of permanent tubes. A regressive process had thus taken place in many cases, loss of the free mode of life and passing to passive nutrition.

A very early divergence evidently took place in the Polychaeta, radiation of nearly all families certainly of all the main groups. In many of these groups, particularly in those living in tubes (Meier, 1893), parallel evolution has taken place (Svetlov, 1962). However, numerous convergent formations of purely adaptive character developed in polychaetes. All this makes it difficult to clarify the phylogenetic relationships in the Polychaeta and, especially, to determine which characters should be considered as primitive. On the basis of the above morphological-functional survey, the following characteristics of benthic Phyllodocidae should be considered as primitive:

1. The strict homonomy of the segments in adult animals. The large and varying number of segments. The uniramous parapodia, with setae of the same type on the entire body and in every bundle; the thin, weak acicula. The tactile function of the body segments are carried out by the dorsal and ventral cirri, which are homonomous on all segments. The integument rich in ciliate epithelium, which forms ciliary rings on the dorsal side.
2. The distinct primary heteronomy of the body. The relatively large number of segments in the larvae.
3. The processes of cephalization in the earliest stages of development: the oral segment is distinctly separated from the cephalic lobe, the anterior segments are little modified and do not become fused into a distinct, specialized peristomium.
4. The subepithelial position of the nervous system. The brain is small in volume and number of cells and is weakly differentiated; the anterior part 67 of the brain is very little developed; centers of association (corpora pedunculata) and palps connected with these centers are absent.
5. Excretory system represented by protonephridia.
6. Intestine and derivatives of the stomodeum weakly developed. Pharynx tubular, without chitinous jaws, mid-intestine without pockets.
7. Vascular system little developed. Cutaneous respiration, absence of branchiae. Hemoglobin dissolved in the nervous system.

8. Epitoky rare, not causing distinct modifications in the morphology of body and segments.

9. Care of progeny weakly developed; fertility and mortality of progeny high.

10. Larval forms pelagic. Except for the usual provisional systems, the orthogonal neuromuscular system, protonephridia, blastocoel, the larvae have no specialized adaptations.

11. Generic differentiation not very distinct.

12. Eurybiontic life of adult forms (presence of benthic and pelagic species in the same family). Active, not selective nutrition of adult and larval forms. Absence of specially constructed shelters (permanent tubes).

Some of the above characteristics of structure and biology of polychaetes which we consider as primitive characters occur in different families, but they are developed to the greatest extent and most markedly in the Phyllodocidae, so that it seems justified to consider them as the most archaic group of the recent Polychaeta.

Position of the Phyllodocidae and related families in the general classification of Polychaeta

The phylogenetic relationships between the different families are not clear, and there is no single detailed and generally accepted classification of the Polychaeta, with division into orders and suborders. Most authors therefore do not mention orders, and orders do not appear in the catalogue of Hartman (1959).

Because of bad preservation, paleontological data are very few, and they are not always beyond doubt (Gekker and Ushakov, 1962). There are often only assumed traces of their activity (paleoichnology). However, some well preserved imprints of polychaetes have been found which prove that there was a diversified fauna of polychaetes as early as in the Lower Cambrian (Walcott, 1911). Deposits several meters thick have been found in the Silurian; they consist of calcareous tubes of the specialized family Serpulidae, and also chitinous jaws of polychaetes, so-called scolecodonts, which differ only slightly from those of the recent Eunicidae. Well preserved imprints of complete Eunicidae (Eunicites) from the Jurassic have been described (Ehlers, 1869). All this proves the great antiquity of polychaetes.

68 Of special interest is the discovery by Glaessner (1958, 1962) in the Lower Cambrian of Australia of a characteristic polychaete, for which he established the new family Sprigginidae. A well preserved imprint was found together with traces of other pelagic animals (medusae), and Glaessner assumed that the worm was related to the Tomopteridae, which seems correct. The species differs from the recent Tomopteridae only in that each podial appendage has only a single seta at the end, while these setae have disappeared in the recent Tomopteridae. Sharov (1965) considers Spriggina floandersi Glaessner as the ancestral form of Spinther. This is not sufficiently justified in our opinion from the morphological and phylogenetic point of view.

Livanov (1940) thinks that among the ancestral forms of the pelagic Phyllodocidae and related families are Canadia and Worthenella, described by Walcott (1911) from the Middle Cambrian of British Columbia.

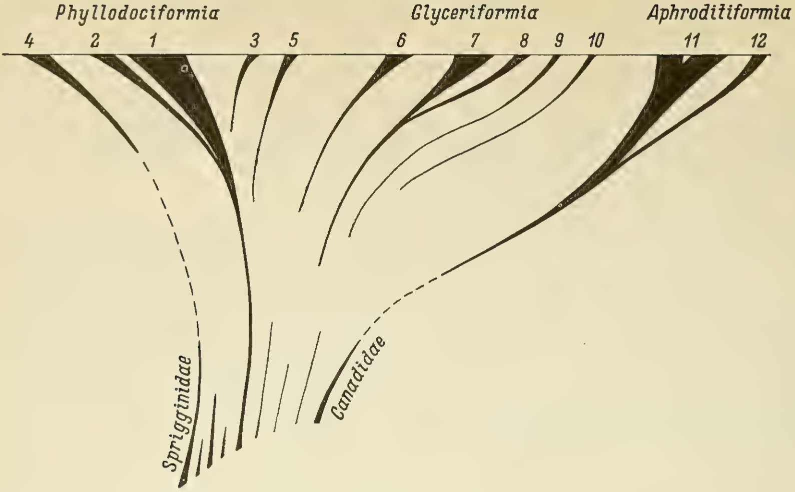

FIGURE 19. Phylogenetic diagram of the Phyllodociformia:

1) Phyllodocidae sensu lato; 2) Alciopidae; 3) Typhloscolecidae; 4) Tomopteridae; 5) Lacydoniidae; 6) Nephthyidae; 7) Glyceridae; 8) Goniadidae; 9) Sphaerodoridae; 10) Pisionidae; 11) Aphroditidae sensu lato; 12) Chrysopetalidae.

The excellent imprint of Worthenella may be provisionally considered as a pelagic polychaete, but Canadia, with its enormous bundles of large setae, is certainly a benthic species, closely resembling the Aphroditidae; the imprint shows no traces of elytra, which are characteristic for the Aphroditidae, but dead Aphroditidae usually lose the elytra, and their body becomes much narrower, i.e. it has exactly the appearance shown in Walcott's photographs. The Canadidae (with only the single genus Canadia), possibly developed into the recent Aphroditidae sensu lato (Figure 19). Fossils of true ancestral Phyllodocidae have not been found, probably because their integument is very delicate and their setae very thin, scarcely visible with the naked eye.

69 Several classifications of recent polychaetes have been published which differ markedly in content. Most German authors (Hemplemann, 1931; Friedrich, 1938; Kaestner, 1955) include the Phyllodocidae in the large suborder Nereimorpha, which contains all the families of errant polychaetes except the Amphinomidae sensu lato, which form a suborder of the order Errantia. In the suborder Nereimorpha the German authors place the Phyllodocidae after the Aphroditidae. In Hartman's catalogue (1959), which does not mention orders, the Phyllodocidae occupy 12th place, after the Aphroditidae and Amphinomidae.

Livanov (1940) gives a slightly different classification, which has been accepted here with some modifications (Ushakov, 1955a). In addition to the Nereimorpha, Livanov established the order Phyllodocemorpha, in which the Phyllodocidae are placed first, followed by the Aphroditidae.

Two new classifications have recently been published, by Dales (1962, 1963), and Mileikovskii (1968). Dales based his classification on specialized organs, derivatives of the stomodeum. He showed that the order Drilomorpha is an artificial group, in which families without close relationship have been placed. Dales established 14 orders, with very unequal numbers of families. His largest group, the Phyllodocida, contains more than 15 families, including the Syllidae, Hesionidae, Pelargidae and Nereidae. The Phyllodocida of Dales' classification are virtually identical with the Nereimorpha, except that Dales placed the Eunicidae sensu lato in a separate group, the Eunicida, together with the Amphinomida and after the Spionida.

Mileikovskii based his classification on the "biogenetic law" and on the structure of the early stages of nectochetes which had completed their metamorphosis. His classification differs from the earlier ones mainly in the introduction of more detailed divisions. He raises the order Amphinomorpha to a superorder, of the same rank as the Errantia and Sedentaria. Dales did not use the division of polychaetes into Errantia and Sedentaria at all.

Comparison of the above classifications shows that there are profound differences between them. Without considerable modifications they retain only the Eunicemorpha, Amphinomorpha and Terebellomorpha; the composition and range of all other groups, and the order in which they appear in the classifications differ markedly. However, the Phyllodocidae occupy first place in both classifications, so that both authors evidently consider the Phyllodocidae as the most primitive family, although they do not state this explicitly.

A quite different position is taken by V. Storch (1968), who accepts the phylogenetic views of O. Storch (1914, 1915), who first published the theory of the primitive nature of the Amphinomidae, which is based on tetraneury. However, Gustafson (1930) stated that tetraneury should be considered as a secondary phenomenon, and not as a primitive character. Tetraneury is 70 given no phylogenetic importance also by Livanov (1940) and Beklemishev (1964). The groundlessness of Storch's views is further proved by the data on the development of the Amphinomidae, published by Sveshnikov and Ts'u Wên-jên (1963), who assumed that only two nerve cords develop originally.

The scheme of relationships between errant polychaetes, described by V. Storch (1968) and based on the principle of "homologous bridges," has, however, some points of interest. Storch considers the Amphinomidae—Aphroditidae as the "central type" and thinks that two different trends of development had taken place in the polychaetes: 1) Nephthyidae—Glyceridae—Phyllodocidae and 2) Chrysopetalidae—Nereidae—Hesionidae—Syllidae. These two trends agree with my view that there are two orders, Phyllodocemorpha and Nereimorpha (see below). As already mentioned during the discussion of the parapodial complexes (p. 36), it is difficult to disagree with the basic position of Storch on the primitiveness of the Amphimonidae. If the scheme of V. Storch (1968, p. 329) is turned 90° to the left, it agrees completely with my concept, and strikingly illustrates the primitive character of the Phyllodocidae, and emphasizes the narrow specialization of the Amphinomidae, which represents a blind alley in the development of polychaetes.

In the context of the views of both Storchs, the work of Sharov (1965) should be mentioned. He thinks that the genus Spinther, which was included in the Amphinomidae in the past, is the most primitive form of polychaetes. Sharov's theoretical concept has been subjected to severe criticism by Manton (1967). It may be remembered that species of Spinther are mainly commensals, living on sponges, and their semiparasitic mode of life could hardly have been an incentive for the development of free-living forms.

The order Phyllodocemorpha is conceived here more narrowly than the Phyllodocida of Dales. The families Syllidae, Hesionidae, Pilargidae

(Otopsidae) and Nereidae, which have true metanephridia, are placed in the order Nereimorpha. The order Phyllodocemorpha (in my concept), as shown in Figure 19, consists of three suborders (or superfamilies): the Phyllodociformia, Glyceriformia, and Aphroditiformia. The first and third suborder were established, but without systematic rank, by Levinson (1882), but have not been accepted by systematists. I accept the Aphroditiformia exactly as defined by Levinson. I place 5 families in the suborder Glyceriformia: the Glyceridae, Goniadidae, Pisionidae, Sphaerodoridae and Nephthyidae. The suborder Phyllodociformia contains the families Phyllodocidae (sensu lato), Alciopidae, Tomopteridae, Typhloscolecidae and Lacydoniidae, which are described in detail in the systematic part.

The Aphroditiformia and partly the Glyceriformia form relatively compact groups, but such a monomorphism is not characteristic for the Phyllodociformia, which contain very archaic families. The Phyllodocidae, which retained the most primitive characteristics of structure, occupy the central position. The family Alciopidae is rather closely related to the recent benthic Phyllodocidae, and they possibly have a common origin with the ancestral forms: Eulalia—Eumida—Pterocirrus (Figure 21). The family Tomopteridae is the most ancient, highly specialized group, and it is difficult to find relationships between them and any recent Phyllodocidae. These 71 two families have a very different morphological organization, in both adult and larval forms. They differ particularly in the number of segments in the larvae (p. 50). The Tomopteridae evidently became separated very early, and adaptations to pelagic life developed in them on entirely different lines than in the Alciopidae. A special place is occupied also by the Typhloscolecidae; their larvae, according to Sveshnikov (p. 50) show a number of specific characters, and some of their provisional organs are retained by the adults (e.g. the prototroch in Typhloscolex). They should probably be considered as neotenic forms adapted to ectoparasitic life, and developed, according to Dales (1955b), from ancestors of free-swimming pelagic Phyllodocidae.

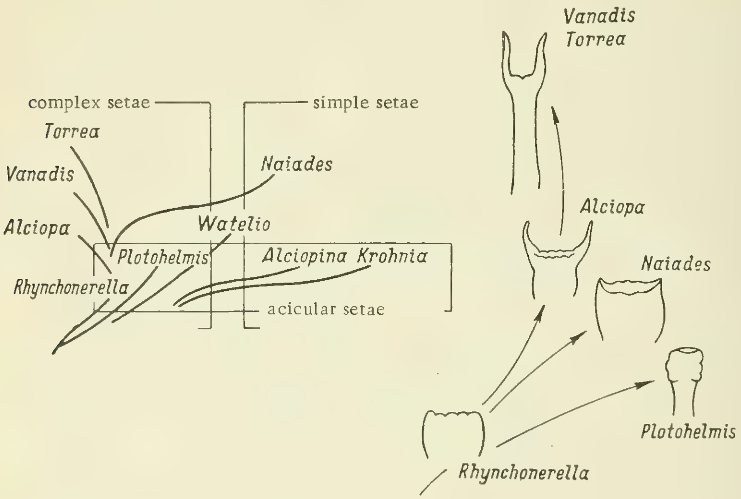

FIGURE 20. Phylogenetic relationships in the Alciopidae (after Dales, 1955)

The few species of the Lacydoniidae, because of the structure of the parapodia and proboscis and the development of the larvae, are intermediate between the Phyllodocidae and the Nephthyidae; they apparently developed from some ancestral Phyllodocidae in which the tendency to form biramous parapodia first appeared in connection with their fossorial mode of life.

The phylogenetic relationships in the family Alciopidae were studied in detail by Dales (1955b). He bases his scheme (Figure 20) on characters of the structure of the proboscis and parapodia.

Phylogenetic relationships in the family Phyllodocidae

The composition of the family Phyllodocidae is interpreted differently by various authors. Bergström (1914), in his monograph of the Phyllodocidae, removed from it and raised to the rank of separate families the Lacydoniidae, Pontodoridae, and Iospilidae. This has been accepted by some authors
72 (Day, 1967). Hartman (1959) established the family Lopadorhynchidae. Fauvel (1923, 1959) considers the Phyllodocidae as a larger family and includes in it all the above four groups as subfamilies.

I agree with Fauvel's classification in principle, but I consider the Lacydoniidae as an independent family. As to the other families, which contain pelagic forms, there is not sufficient reason to consider them as families, and I consider them as subfamilies of the family Phyllodocidae sensu lato. Numerous aberrant characters in the pelagic forms are due mainly to adaptations to life in the water. The well studied development of Lopadorhynchus differs little from that of other benthic Phyllodocidae (p. 49). The very long podial appendages of Pontodora pelagica (the only species of the subfamily Pontodorinae) should be considered as adaptations. It is interesting that the characteristic, chitinous hooks in the pharynx, which are absent in all other genera, developed also in Phalacrophorus (subfamily Iospilinae) and in Pelagobia (subfamily Lopadorhynchinae). These chitinous hooks are convergent developments to hold the prey. The subfamily Lopadorhynchinae is apparently of heterogeneous composition, containing genera of different origin (see below). The fact that the family Phyllodocidae sensu lato, together with numerous benthic forms of uniform morphology, contains also markedly adapted pelagic species agrees with the archaic character of this family, which did not develop a narrow specialization.

The subfamilies Phyllodocinae, Mystidinae, Protomystidinae, Lugiinae and Eteoninae, established by Bergström (1914), were not accepted by later authors. I also reject them, as they have no phylogenetic significance. Only Hartmann-Schröder (1963) uses the name Eteoninae, including in it the genera Mystides, Eteonides, Eteone and Mysta. The relationship of these genera is rather artificial, since there is only one pair of tentacular cirri on the 1st segment in Mystides—Eteonides while Eteone—Mysta have two pairs, which distinguishes them sharply from all other benthic Phyllodocidae. The above subfamily may have to be retained for genera with two pairs of tentacular cirri on the 1st segment, and in this case should evidently contain the pelagic Pelagobia and, possibly, Maupasia and Pedinisoma. But this requires a comparative anatomical study of the nervous system and a more detailed description of the structure of the anterior segments.

Generic differentiation is not always distinct in the Phyllodocidae. Generic characters are the following: the number and arrangement of the tentacular cirri, the extent of reduction and fusion of the anterior segments, the number of cephalic tentacles and the structure of the proboscis. The form of the tentacular cirri has sometimes also to be considered.

The proboscis is rather variable and sometimes shows marked variation in the same genus. Convergent structures have been found in entirely different genera. Thus, large lateral papillae at the distal end of the proboscis are present in the subgenus Mysta of the genus Eteone and in
73 Notophyllum, which in our classification is situated on the opposite side of the phylogenetic tree. In the genus Eulalia are the species E. semenovi and E. sotniki from the Antarctic (Averintsev, 1972), which should be placed in the genus Austrophyllum because of the characteristic arrangement of the papillae on the distal part of the proboscis (in 6 rows), but this is not possible because of the absence of an additional aciculum which is characteristic for Austrophyllum. Chitinous hooks on the pharynx of Phalacrophorus and Pelagobia, which belong to different subfamilies, are also a convergent character (Figure 5). The proboscis thus does not always give a reliable criterion for the establishment of genera. The proboscis of the Alciopidae, which is a more specialized family, shows clearly the phylogenetic relationships in the family (Figure 20), but this is not the case in the Phyllodocidae. The proboscis has not developed the final generic specialization, which agrees with the other primitive characteristics of this family.

The form of the tentacular cirri on the anterior segments, used for the definition of the genera Eulalia—Steggoa and Eumida—Pterocirrus, is a very doubtful character (especially in fixed material). In specimens of Eulalia viridis and Eumida sanguinea, in which the ventral tentacular cirri on the 2nd segment are spindle-shaped, the cirri may become flattened in females during the period of sexual maturity. In the species of the primitive genera Protomystides and Mystides, the ventral cirri of the 2nd segment have a very varying form. Thus, the form of the tentacular cirri is of little phylogenetic significance, but this character is sometimes useful for the division of genera with a large number of species. There is a recent tendency among systematists to divide taxonomic groups into ever smaller units.

The most important character for the diagnosis of genera is the structure of the anterior segments and the cephalic lobe, i.e. the degree of cephalization. This character makes it possible to determine phylogenetic relationships in the entire family. Bergström had proposed to use a formula for describing the anterior segments, and this has been widely used since. An example of such a formula is $1 + O\,\frac{o1}{a1} + S\,\frac{a\,1}{aN}$, in which the plus sign separates the segments, the dorsal podial appendages are the numerator and the ventral appendages the denominator, 1 represents a tentacular cirrus, N a normal podial cirrus, S a bundle of setae, a the acicula, and O and o the absence of setae and of acicula. The formula thus indicates that there is only one pair of tentacular cirri on the 1st segment, 2 pairs on the 2nd segment, but no setae, and acicula only at the ventral tentacular cirri; on the 3rd segment there is one pair of dorsal tentacular cirri, and one pair of normal ventral cirri, a podial lobe with setae, and acicula on the dorsal and ventral appendages.

As a large new material shows, the presence or absence of acicula at the base of the tentacular cirri is not a generic character, but it may be a character for the determination of species. The setae on the 2nd and 3rd segment are also sometimes without diagnostic value, because their presence 74 or absence in some species is connected with age. Of much greater importance for the definition of genera is the degree of reduction and fusion of the anterior segments, and the classification of families in this work is based on this character. I omit, therefore, in the diagnoses of genera in Bergström's formula the indication of the presence or absence of acicula, especially since it cannot always be determined, and introduce into the formula some additional symbols. If the anterior segment is reduced dorsally, and partly fused with the 2nd segment, we place the first two anterior segments in parentheses, for example, in the case of Eumida: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. No parentheses indicates that all segments are fully developed and distinctly demarcated; if only the right parenthesis is given, it indicates that the cephalic lobe is fused to some extent with the circumoral segment. If specialized, hook-shaped setae are present on the anterior segments, I substitute C for S to emphasize the specific character of the genera.

We have to evaluate the degree of reduction of the anterior segments unfortunately only by the external characters, which do not always give a clear picture. For more precise determination of the degree of cephalization, as was stated already by Pruvot (1883, 1885), a detailed study of the nervous system of the anterior segments in different species of Phyllodocidae would be necessary and would prove the more exact relationships between the genera. Bergström's illustrations of the nervous system are too schematic (he had apparently not completed this part of his work). However, he observed that a reduction of the nerve roots of the subpharyngeal commissures has taken place in Eteone, which innervate the first pair of tentacular cirri in other Phyllodocidae. Bergström stated that the 1st segment is completely fused with the 2nd, in Eteone, and that only two pairs of tentacular cirri of the 2nd segment are retained. If that is the case, Eteone is on a higher level of development than many other genera of Phyllodocidae. However, Bergström's observations have not been confirmed by the study of the larval forms. In the metatrochophores of Eteone, the longer first (oral) larval segment with two pairs of tentacular cirri is formed immediately (p. 46). The presence of two pairs of tentacular cirri on the 1st segment of Eteone is evidently a primitive character, inherited from ancestral forms in which all segments had the same number of podial appendages.

We think that the anterior (circumoral) segments differed little at first from the following segments in the primitive Phyllodocidae, and that first the 1st, then the 2nd, and finally the 3rd segment became modified during evolution: long tentacular cirri developed as tactile organs, directly connected with the functions of the cephalic lobe. An evolutionary process like the multiplication of the tentacular cirri could have taken place only in the more primitive forms, which had homonomous body segments. The following stage of cephalization had to be partial fusion of the two anterior segments; but the Phyllodocidae have not reached the stage of development of a distinct peristomium together with integration of the number of tentacular cirri, which has taken place in the Aphroditidae and Nereidae.

The primitive Phyllodocidae had only two pairs of frontal tentacles. The 75 single median tentacle appeared at a considerably later stage of development.

This is proved by the ontogenesis: in all forms which have 5 cephalic tentacles in the adult, the median single tentacle is still absent in the early stages of the nectochete. However, the number of tentacular cirri is the same at that stage as in the adults. Thus, all nectochetes of Phyllodoce and Eulalia have 4 pairs of tentacular cirri, the nectochetes of Mystides have 3 pairs, and the nectochetes of Eteone 2 pairs.

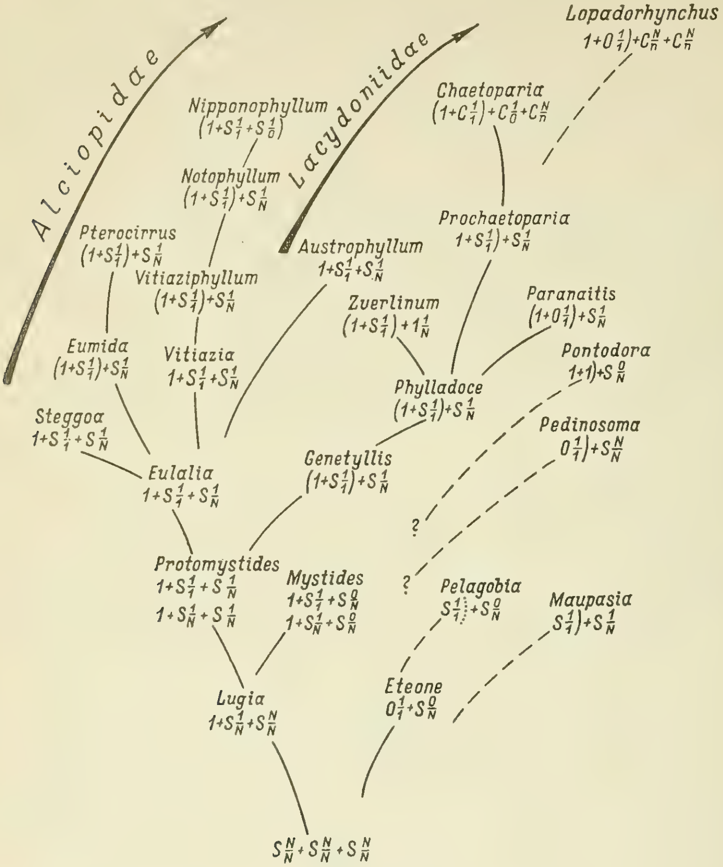

FIGURE 21. Phylogenetic relationships in the Phyllodocidae

The most likely hypothetical original form is Lugia (Figures 2, 3, and 21). This small species, which lives at small and great depths, has only two modified anterior segments, without fusion or reduction. A further complication is observed in the genus Protomystides: the first three anterior segments already have tentacular cirri, but all segments are clearly demarcated. The primitive character of these genera is also emphasized by the structure of the parapodia, the absence of distinct cirrophores, which are present in most other Phyllodocidae; the fifth median cephalic tentacle is
76 absent in these genera. The genus Mystides, also, retains some primitive characters, but it is isolated to some extent, as only the dorsal cirri on

the 3rd segment have disappeared, which has become fixed in the ontogeny. An analogous phenomenon is present in the genus Sphaerosyllis of the family Syllidae; the cause of disappearance of the dorsal cirri on the 3rd segment in these two genera, which belong to different families, is not known.

The central place in the benthic Phyllodocidae is occupied by two genera: Eulalia and Phyllodoce, which formed two independent trends of development which are parallel to a large extent. We included in the "Eulalia" group genera with 5 cephalic tentacles; it is easy to trace in this group, from Eulalia sensu stricto to Eumida and Pterocirrus, the gradual fusion of the two anterior segments and their partial reduction, and in the line: Vitiazia—Notophyllum—Nipponophyllum, also the appearance of nuchal organs and of the primordia of the notopodia in the form of an additional aciculum and 1 or 2 notopodial hairlike setae. The highest degree of cephalization in this group is present in Nipponophyllum (p. 162).

The group "Phyllodoce" contains genera in which the median tentacle is absent, but an occipital papilla behind the cephalic lobe forms its homologue. Biramous parapodia also appear in this group, in the genus Zverlinum, established by Averintsev from material from the Antarctic for Austrophyllum monroi Hartman. The notopodia evidently developed independently and parallel in both groups. Fusion of the anterior segments is most distinct in this group in the genus Paranaitis, which has a characteristic "collar," and in the genus Chaetoparia with markedly modified anterior segments with simple hook-shaped setae. The genus Chaetoparia is connected through the intermediate genus Prochaetoparia, with the central genus Phyllodoce.

Eteone has an isolated position in the classification of benthic forms. It has 2 pairs of tentacular cirri on the 1st segment, where all other benthic genera of Phyllodocidae have only one pair of cirri. If 2 pairs of tentacular cirri on the 1st segment are the result of fusion of the two anterior segments, as was assumed by Bergström (see above), Eteone partly resembles the Aphroditidae in this respect and is possibly one of their ancestral forms, i.e. Eteone occupies one of the highest steps on the hierarchical ladder of the family Phyllodocidae. On the other hand, if it is assumed that one pair of tentacular cirri on the 1st segment developed in all other genera as a result of integration of the two pairs of cirri which are present on this segment in the ancestral forms, Eteone is a more primitive genus than the others. In any case, Eteone has an isolated position.

The above phylogenetic relationships are represented diagrammatically in Figure 21. Completely different views are held by Bergström: He thinks that the primitive type of parapodia in the Phyllodocidae was biramous, and considers the genus Notophyllum as the origin of development of the whole family Phyllodocidae. This position, however, cannot be accepted, since Notophyllum is one of the most highly specialized genera, in which the degree of cephalization of the anterior segments has progressed very far.

The systematic position of the pelagic forms, many of which show characters of high specialization, is not clear. The genus Lopadorhynchus closely resembles in some characters — fusion of the cephalic lobe with the
77 anterior segments, the presence on these segments of specific golden hook-shaped setae — the benthic genus Chaetoparia, which is connected through the intermediate genus Prochaetoparia with the central genus

Phyllodoce. Dales (1955b) suggested that Lopadorhynchus may have developed from Protomystides and Mystides, but he did not give any proof. On the other hand, the genera Pelagobia and Maupasia, of the subfamily Lopadorhynchinae, closely resemble the benthic genus Eteone in the structure of the anterior segments (two pairs of tentacular cirri on the 1st segment). These two genera possibly form a distinct branch of the family Phyllodocidae together with Eteone, independent of Lopadorhynchus, which has not attained wide development. The systematic position of the pelagic genus Pedinosoma, of the same subfamily, is not clear because the structure of its anterior segments has been differently interpreted by various authors (p. 181). The same is the case with the genera Phalacrophorus and Pontodora, which belong to different subfamilies. The pelagic genera thus do not form a compact group and may possibly have a different origin.

Some authors (Reibisch, 1895; Gravier, 1896) think that the pelagic Phyllodocidae are the ancestral forms of the benthic Phyllodocidae. This seems unlikely. All pelagic Phyllodocidae, due to the special conditions of existence, are highly specialized, and it is difficult to assume that they could have developed into the more primitive genera of benthic Phyllodocidae, which have proved to be the ancestors of other polychaetes. It seems more correct to assume that the pelagic Phyllodocidae developed from the benthic Phyllodocidae, probably from different ancestors, and are a blind alley of development, as shown in Figure 21.

The diagram of relationships proposed is provisional, but may serve as a working hypothesis for further research.

ZOOGEOGRAPHICAL NOTES

We will now discuss the geographical distribution of the Phyllodociformia, separately for the benthic and the pelagic species.

Benthic species (maps 1–7).* Fifteen species of Phyllodocidae have been recorded from the Polar Basin (table on pp. 77–82). The family Lacydoniidae does not occur there. Three species are endemic in the Arctic: Protomystides occidentalis – Davis Strait, depth 580 m; Eumida minuta – Davis Strait, 122 m, Laptev Sea, 45–65 m, Chukchi Sea, 29–135 m; Pteroccirus slastnikovi – Laptev Sea, 22–869 m. Another mainly arctic species is Paranaitis wahlbergi, although it has been recorded from the North Sea (Friedrich, 1938). This species is possibly replaced in the North Sea by P. kosteriensis (Malmgren) (p. 135). All other species recorded from the Polar Basin have a wider geographical distribution and also occur in northern parts of the Atlantic and Pacific. They are apparently
81 circumpolar. The most common species in the Polar Basin are Phyllodoce (Anaitides) groenlandica, Ph. (A.) citrina, Eteone longa, E. flava, E. spetsbergensis spetsbergensis, E. (Mysta) barbata and partly Eulalia bilineata. The distribution of Phyllodoce (Anaitides) maculata and Eumida sanguinea is much more restricted. They spread into the Arctic only in the Barents and White seas; they have so far not been found east of Novaya Zemlya, but inhabit the northern

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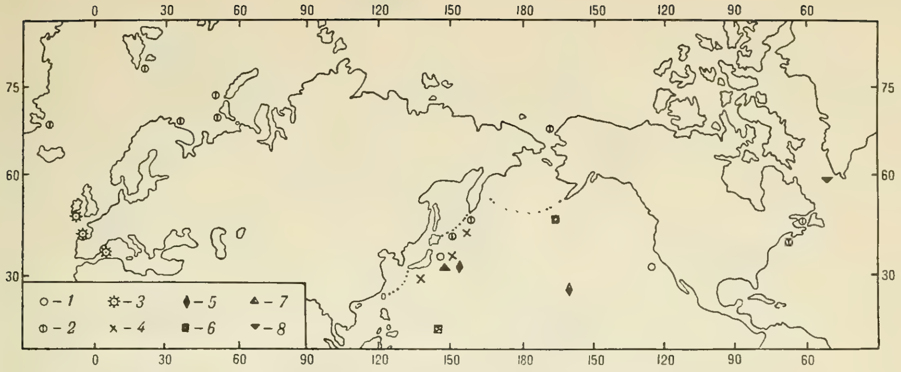
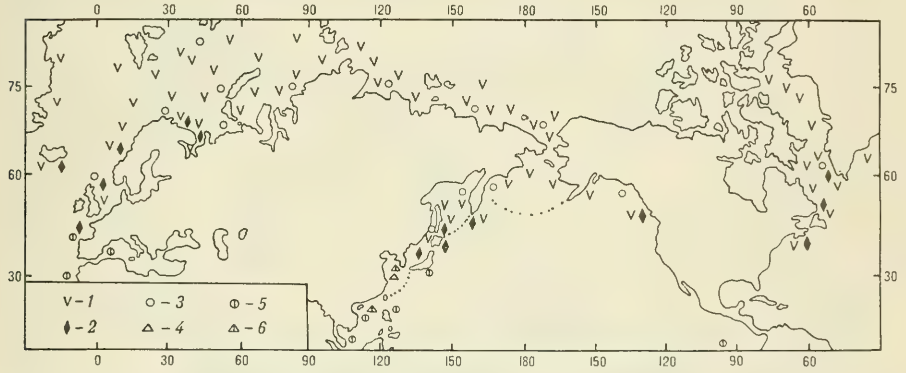
* The maps show only the main regions of occurrence.



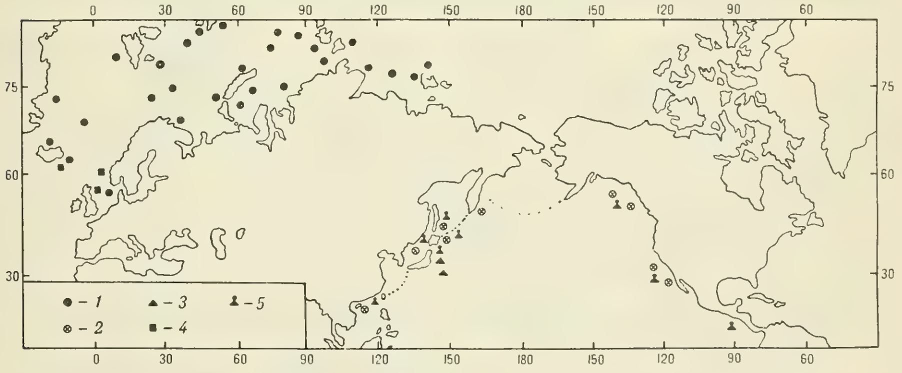
MAP 1. Distribution of species of Lugia Quatrefages, Mystides Théel, and Protomystides Czerniavsky:

1) Lugia abyssicola; 2) Mystides borealis; 3) M. borealis coeca; 4) M. rarica; 5) M. schroderae; 6) Protomystides levensteinae; 7) Pr. orientalis; 8) Pr. occidentalis.



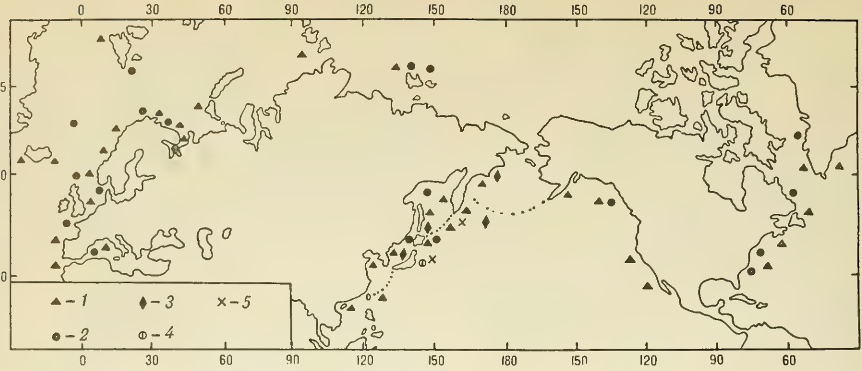
MAP 2. Distribution of species of Phyllodoce Savigny:

1) Phyllodoce (Anaitides) groenlandica; 2) Ph. (A.) maculata; 3) Ph. (A.) citrina; 4) Ph. (A.) chinensis; 5) Ph. (A.) madeirensis; 6) Ph. (A.) papillosa.



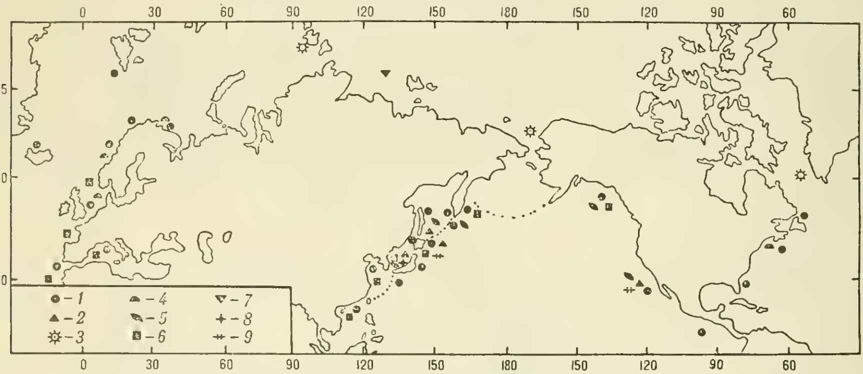
MAP 3. Distribution of species of Paranaitis Southern and Genetyllis Malmgren:

1) Paranaitis wahlbergi; 2) P. polynoides; 3) P. caecum; 4) Genetyllis lutea; 5) G. castanea.



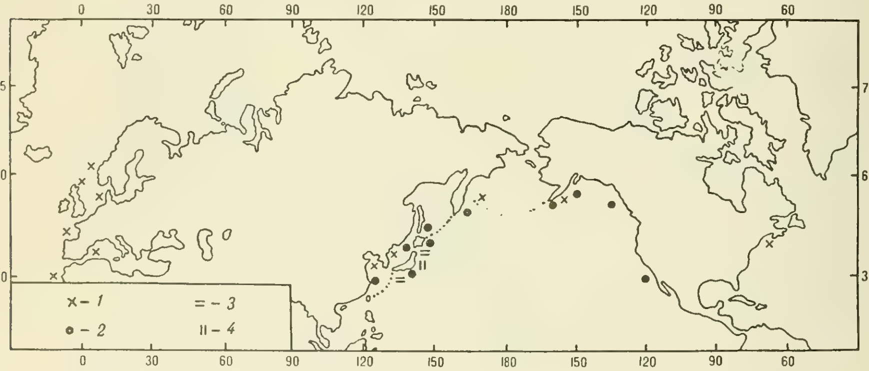
MAP 4. Distribution of species of Eulalia Savigny:

1) Eulalia viridis; 2) E. bilineata; 3) E. sigeformis; 4) E. austrophylloformis; 5) E. gravieri.



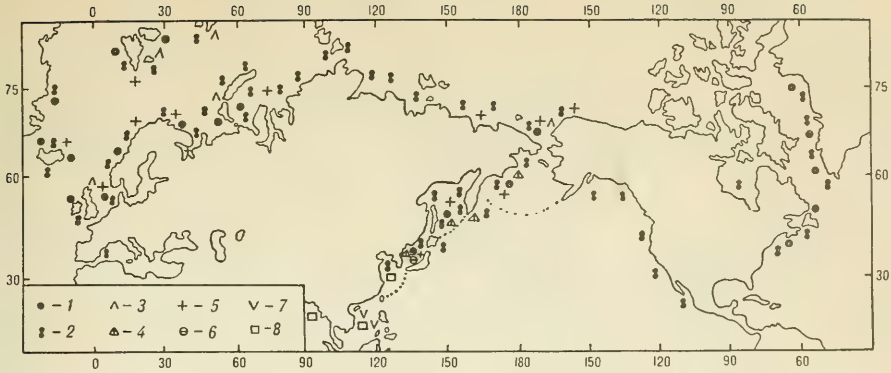
MAP 5. Distribution of species of Eumida Savigny and Pterocirrus Claparède:

1) Eumida sanguinea; 2) E. tubiformis; 3) E. minuta; 4) E. fusigera; 5) E. nigrimaculata; 6) Pterocirrus macrocerros; 7) P. slastnikovi; 8) P. notoensis; 9) P. imajimai.



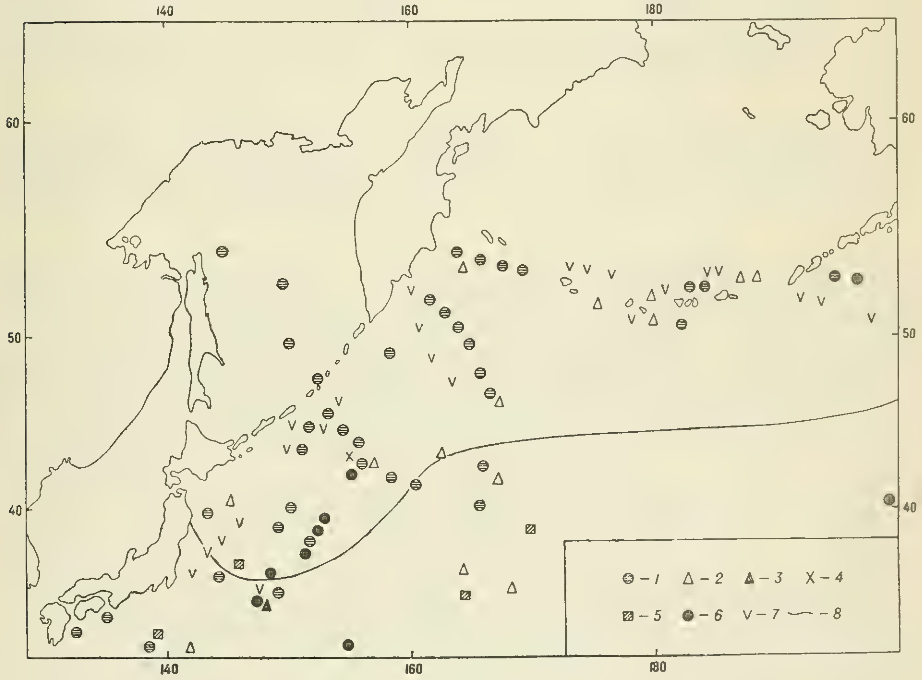
MAP 6. Distribution of species of Notophyllum Oersted and Nipponophyllum Imajima and Hartman:

1) Notophyllum foliosum; 2) Not. imbricatum; 3) Nipponophyllum japonicum; 4) Nip. sagamianum.



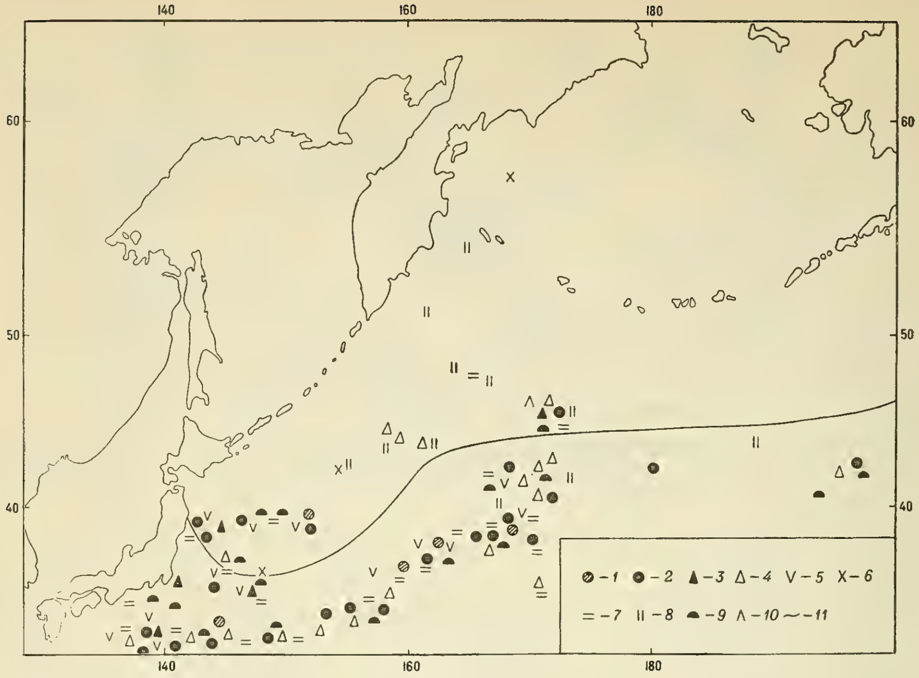
MAP 7. Distribution of species of Eteone Savigny sensu lato:

1) Eteone flava; 2) E. longa; 3) E. spetsbergensis spetsbergensis; 4) E. spetsbergensis bistriata; 5) E. (Mysta) barbata; 6) E. (M.) ornata; 7) E. (M.) maculata; 8) E. (M.) tchangsii.



MAP 8. Distribution of pelagic Phyllodocidae in the Northwest Pacific:

1) Pelagobia longicirrata; 2) Maupasia caeca; 3) M. brodskyi; 4) Lopadorhynchus appendiculatus; 5) L. uncinatus; 6) Pontodora pelagica; 7) Phalacrophorus pictus; 8) mean annual 5° isotherm at a depth of 400 m.

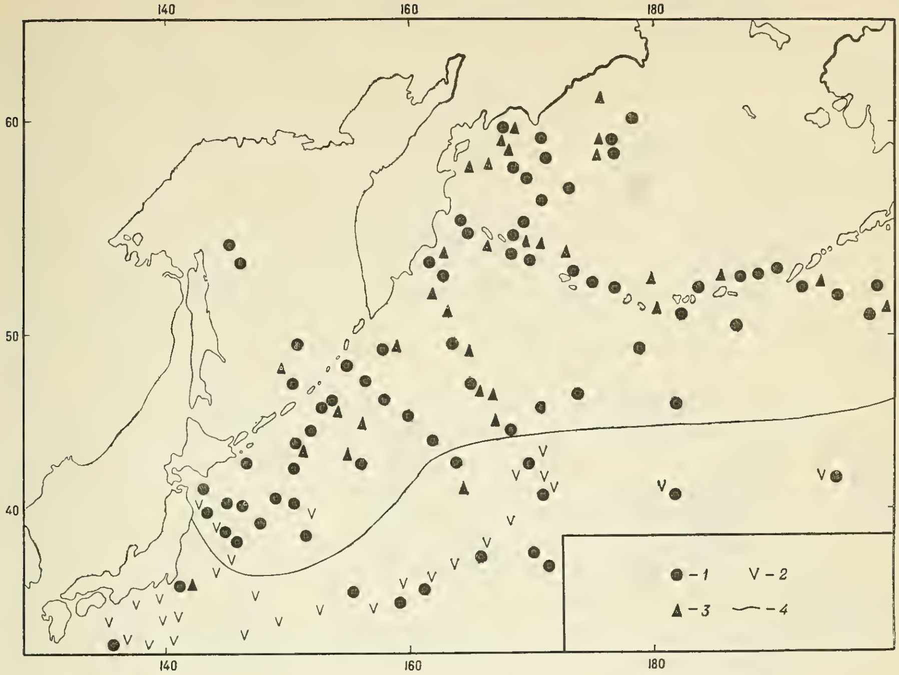


MAP 9. Distribution of Alciopidae in the Northwest Pacific:

1) Vanadis formosa; 2) V. longissima; 3) Alciopina parasitica; 4) Plotohelmis tenuis; 5) Krohnia lepidota; 6) K. exellata; 7) Rhynchonerella gracilis; 8) Rh. angelini; 9) Rh. petersii; 10) Alciopa reynaudii; 11) mean annual 5° isotherm at a depth of 400 m.

parts of the Pacific Ocean; P. (A.) maculata reaches the west coast of Greenland and Hudson Bay in North America, and E. sanguinea the Gulf of St. Lawrence. Notophyllum foliosum also does not enter arctic waters; it occurs in the Mediterranean, the North Sea, the Norway Sea and the Atlantic Ocean near the coast of New England; it has been recorded from the North Pacific near Alaska, Bering Island, in the Sea of Japan and the Yellow Sea. Pterocirrus macroceros also has an amphiboreal distribution: Mediterranean, west coast of Africa, European coast of the Atlantic Ocean, Sea of Japan, Yellow Sea and South China Sea, Pacific coast of Canada.

The fauna of benthic Phyllodocidae in the Far Eastern seas (Bering Sea, Sea of Okhotsk and Sea of Japan) is richer than that of the Polar Basin. Not including the coasts of Japan and the open parts of the Northwest Pacific, 22 species have been recorded in this area, of which 8 species occur also in
82 the Polar Basin. Some of these species are widely distributed in the Pacific: Paranaitis polynoides, Eumida tubiformis, E. nigrimaculata and Notophyllum imbricatum. Endemic species are not numerous in the Far Eastern seas. They are: Eulalia sigeformis, so far found only in the Sea of Japan at a depth of 480–936 m, in the Sea of Okhotsk at 443–645 m, in the Bering Sea at 510 m and in the Aleutian depression at



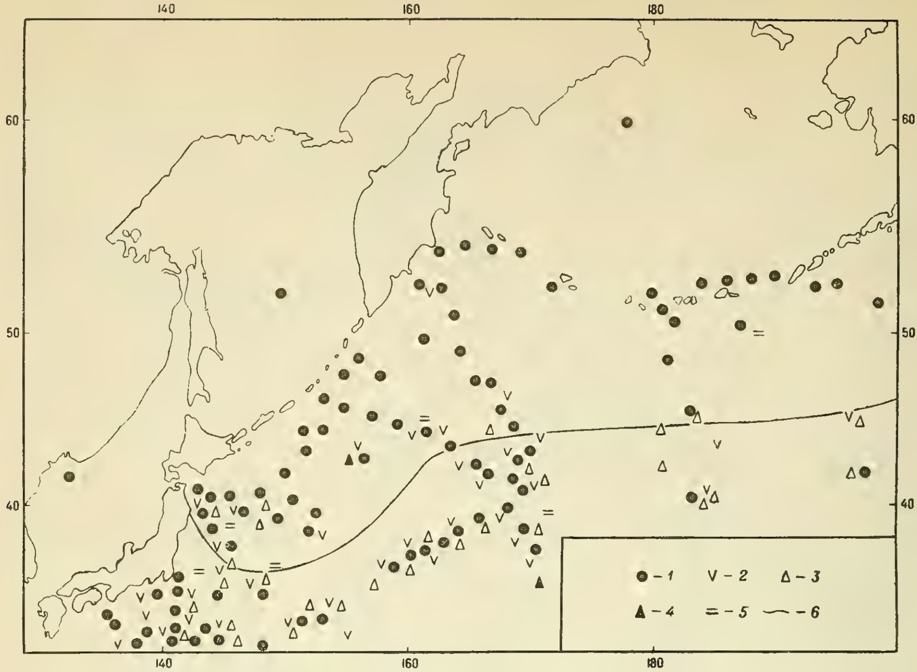
MAP 10. Distribution of Tomopteridae in the Northwest Pacific:

1) Tomopteris septentrionalis; 2) T. elegans; 3) T. (Johnstonella) pacifica Izuka; 4) mean annual 5° isotherm at a depth of 400 m.

2685–7185 m. Phyllodoce laminosa brevis possibly has a still more restricted distribution; it was described by Zaks (1933) from the Sea of Japan (Peter the Great Bay). Eteone spetsbergensis spetsbergensis, which is widely distributed in the Arctic, is replaced in the Far Eastern seas by E. spetsbergensis bistriata, but there is apparently no distinct boundary between these two subspecies in the Chukchi Sea; E. spetsbergensis pacifica (p. 169) inhabits the North American coast of the Pacific.

Fifteen species have been recorded from the coastal waters of Japan (Imajima and Hartman, 1964; Imajima, 1967), of which the following have not been found in the Far Eastern seas: Phyllodoce japonica Imajima, ? Ph. macrolepidota Schmarda, Ph. violacea Treadwell (? = Ph. pruvoti Fauvel), Ph. (Anaitides) elongata Imajima, Ph. (A.) madeirensis Langerhans, Nipponophyllum japonicum (Marenz.) and N. sagamianum (Izuka). This marked difference between the fauna of Phyllodocidae in the Far Eastern seas and the littoral of Japan is due to the
83 relatively cold waters in the Far Eastern seas, while the coasts of Japan are warmed by the Kuroshio stream coming from the south.

The fauna of Phyllodocidae of the Yellow Sea differs markedly from that of the Far Eastern seas. Of the northern forms only Eteone longa occurs here. Phyllodoce (Anaitides) groenlandica and Ph. (A.) maculata,



MAP 11. Distribution of Typhloscolecidae in the Northwest Pacific:

1) Typhloscolex muelleri; 2) Sagitella kowalewskii; 3) Travisiopsis lobifera; 4) T. levinseni; 5) T. lanceolata; 6) mean annual 5° isotherm at a depth of 400 m.

which occur in many parts of the Sea of Japan, are replaced in the Yellow Sea by Ph. (A.) chinensis and Ph. (A.) papillosa. In the littoral of the Yellow Sea appear the large Eteone (Mysta) tchangsii, which also occur in the South China Sea and apparently on the coasts of India. As already noted in the review of the Errantia (Ushakov and Wu Pao-ling, 1965), there is a replacement of one fauna by another in the Yellow Sea, the southern warm-water forms predominating in the upper, warmer horizons (littoral and sublittoral), while in the deeper horizons, due to the cold water at the bottom, some cold-water forms persist, isolated from their main range (relict forms).

The South China Sea (Hainan, Gulf of Tonkin) contains in all areas examined mainly a warm-water fauna. Phyllodoce malmgreni and Ph. (Anaitides) madeirensis have been found only here.

A specific fauna of Phyllodocidae has been found at great depths in the
84 open parts of the Northwest Pacific. We found here: Lugia abyssicola, Mystides rarica, M. schroderae, Protomystides levensteinae, P. orientalis, Paranaitis caecum, Eulalia austrophylloformis, E. gravieri, Pterocirrus imajimai, Vitiazia dogieli, Vitiaziphyllum nuchalum and Eteone vitiazi. New genera had to be established for two of these species.

A comparison of the specific composition of Phyllodocidae in the Far Eastern seas with that of the coast of California is of interest. Some authors (Moore, 1906, 1909a, 1909b; Chamberlin, 1919a; Hartman, 1936a; and others) described numerous species of Phyllodocidae from the area of California. According to Hartman (1968), there are at least 35 species of Phyllodocidae in this region. However, a revision of these species has not been made. Only 8 of these 35 species occur also in the Far Eastern seas: Phyllodoce (Anaitidea) groenlandica, Eulalia viridis, Eumida sanguinea, E. tubiformis, E. nigrimaculata, Genetyllis castanea, Notophyllum imbricatum and Paranaitis polynoides. This suggests that there are few faunistic connections between the Far Eastern seas and the coast of California. Among the above forms, some are amphi-Pacific (with an interrupted range), particularly Eumida tubiformis and E. nigrimaculata.*

Most pelagic polychaetes have an even wider distribution than the benthic Phyllodocidae. Many of them occur in the warm waters of the Atlantic, Indian and Pacific oceans, their distribution is circumtropical and some of them have virtually a worldwide distribution. The composition and distribution of pelagic polychaetes in the northern parts of the Atlantic and Pacific have been described by Støp-Bowitz (1948), Treadwell (1943), Dales (1957), Tebble (1962) and Mileikovskii (1962, 1969). We have given a summary of our data and those of other authors on the main species of pelagic polychaetes of the Northwest Pacific in maps 8–11.

Pelagic Phyllodocidae (Map 8) are represented by only a few species. One of the most common and widely distributed species is Pelagobia longicirrata. It is apparently cosmopolitan. It has been recorded from the central parts of the Polar Basin, and it is not rare in the Northwest Pacific. Phalacrophorus pictus has a similarly wide distribution. Maupasia and Lopadorhynchus are much rarer in plankton and they do not occur in the Polar Basin. The new species Maupasia brodskyi was described from the Northwest Pacific, and has not been found anywhere else. The widely distributed species M. caeca also occurs in this area. There are isolated records of Lopadorhynchus nationalis, L. uncinatus, L. krohnii and L. brevis from subtropical waters near Japan (Dales, 1957; Tebble, 1962); a single specimen of L. appendiculatus was found in our material from the frontal zone of the Kuroshio south of the Kurils; it was previously known only from the Atlantic Ocean and the Mediterranean. At several stations south of the Kurils, Pontodora pelagica was found
85 which also had not been recorded from this region (it had been recorded from the equatorial regions of the Atlantic Ocean and the eastern Pacific, from Canada to Peru). Pedinosoma curtum is very rare; it was described from the tropical and subtropical regions of the Atlantic Ocean, and there were isolated records from the Pacific. The most common species in the North Pacific are: Pelagobia longicirrata, Maupasia caeca and Phalacrophorus pictus, which spread far into the cold waters of the north (map 8; all maps show the mean annual 5° isotherm at a depth of 400 m; it has been taken from the Marine Atlas, Vol. 2, Leningrad, 1953).

The family Alciopidae contains mainly tropical and subtropical species. The Alciopidae do not form mass concentrations, and only isolated specimens have been found. The largest numbers have been recorded for Vanadis longissima, 21 specimens per 1000 m^3 (Tebble, 1962). Most species have been found in the upper horizons; only V. tagensis apparently occurs in the deep layers. Over 15 species have been recorded from the Northwest Pacific, and Vanadis longissima, Rhynchonerella gracilis, Rh. angelini, Plotohelmis tenuis and Krohnia lepidota are the most common. The species distributed farthest to the north (to the Aleutians) is Rhynchonerella angelini. Krohnia excellata has been described from the Northwest Pacific (Kurils); it was later found also in the Bering Sea. It is possibly specific for the cold waters of the Northwest Pacific. Alciopidae have not been found in the Polar Basin.

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* The amphi-Pacific distribution of polychaetes was discussed by me in detail in a recent article (J. Fish. Res. Bd. Canada, Vol. 29, No. 10. 1971).

The Tomopteridae are pelagic polychaetes which occur in the largest numbers. From the northern part of the Pacific Ocean (north of 30° N) the following species have been recorded: Tomopteris elegans, T. septentrionalis, T. planctonis, T. ligulata, T. nisseni, T. (Johnstonella) apsteini and T. (J.) pacifica. Particularly common in the Northwest Pacific are: T. elegans, T. septentrionalis and T. (Johnstonella) pacifica (map 10). T. elegans occurs mainly in subtropical waters, the other two species in the Sea of Okhotsk and the Bering Sea. T. septentrionalis is widely distributed, but T. (Johnstonella) pacifica is restricted to the relatively cold waters of the northern part of the Pacific. The numbers of T. elegans in the northeastern areas of the Pacific may attain 500 specimens per 1000 m^3 (Tebble, 1962). The Tomopteridae also spread into the North Atlantic, and some of them into the Arctic. T. septentrionalis and T. (Johnstonella) helgolandica have been recorded from the Barents Sea and T. planctonis, T. nisseni, T. cavallii, T. krampi and T. septentrionalis from Davis Strait.

The Typhloscolecidae are not numerous, but are widely distributed. There are 5 species in the northwestern part of the Pacific Ocean (map 11); the most common species is Typhloscolex muelleri, which occurs in the Sea of Okhotsk, in the Bering Sea and in the Barents Sea. Sagitella kowalewskii and representatives of the genus Travisiopsis are apparently abyssal species.

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Species	Baltic Sea including the Skagerrak	North Sea	Norway Sea	Baffin Bay and Davis Strait	Greenland Sea and Polar Basin	Barents Sea	White Sea	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Bering Sea	Sea of Okhotsk	Sea of Japan	Yellow Sea	South China Sea	Northwest Pacific	Remarks
Phyllodocidae																		
Lugia abyssicola	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	California
Mystides borealis	—	+	—	+	—	+	—	—	—	—	+	—	+	—	—	—	—	Gulf of St. Lawrence – Gulf of Maine
M. rarica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Kermadec I.
M. schroderae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
M. southerni	+	—	—	—	—	—	?	—	—	—	—	—	—	—	—	—	—	
Protomystides levensteinae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	South of Aleutian Is., Mariana Is.
P. orientalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Tasman Sea, near New Zealand
P. occidentalis	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	
Genetyllis lutea	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
G. castanea	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	Subtropical and tropical parts of the Pacific and Indian oceans
Phyllodoce laminosa laminosa	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	Atlantic coast of Europe, Mediterranean
Ph. laminosa brevis	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	
Ph. gracilis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	?	—	—	Tropical parts of the Pacific and Indian oceans
Ph. malmgreni	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	Same
Ph. (Anaitides) groenlandica	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	Arctic-boreal species
Ph. (A.) maculata	+	+	+	+	—	+	+	—	—	—	—	+	+	+	—	—	—	Amphiboreal species
Ph. (A.) mucosa	+	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Mediterranean
Ph. (A.) citrina	+	+	—	+	—	+	+	+	+	+	+	+	+	+	—	—	—	Gulf of Alaska, Pacific coast of Canada
Ph. (A.) chinensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	

GEOGRAPHICAL DISTRIBUTION (continued)

Species	Baltic Sea including the Skagerrak	North Sea	Norway Sea	Baffin Bay and Davis Strait	Greenland Sea and Polar Basin	Barents Sea	White Sea	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Bering Sea	Sea of Okhotsk	Sea of Japan	Yellow Sea	South China Sea	Northwest Pacific	Remarks
Phyllodoce (A.) madeirensis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	Widely distributed, mainly tropical species
Ph. (A.) papillosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	?	—	? California
Paranaitis wahlbergi	+	+	+	—	+	+	—	+	+	—	—	—	—	—	—	—	—	Mainly arctic species
P. polynoides	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	+	+	West coast of Canada, California
P. caecum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Chaetoparia nilssoni	+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
Eulalia viridis	+	+	+	+	—	+	+	+	—	—	—	+	+	+	+	+	+	Widely distributed, mainly in boreal and subtropical waters
E. bilineata	+	+	+	+	+	+	+	+	+	—	—	—	+	+	—	—	+	Mediterranean
E. sigeformis	—	—	—	—	—	—	—	—	—	—	—	+	+	+	—	—	—	
E. austrophylloformis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
E. gravieri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Steggoa pacifica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Eumida sanguinea	+	+	+	—	—	+	+	—	—	—	—	—	+	+	+	+	+	Mainly boreal species
E. albopicta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	Nicobar Is. (Indian Ocean)
E. tubiformis	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	—	+	California
E. minuta	—	—	—	+	—	—	—	—	+	—	+	—	—	—	—	—	—	
E. fusigera	+	+	+	—	+	—	—	—	—	—	—	—	—	—	—	—	—	Mediterranean, Massachusetts Bay
Eumida nigrimaculata	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	+	Vancouver I., California
Pterocirrus macroceros	+	+	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	Black Sea and Mediterranean, W. Africa, Pacific coast of Canada
P. slastnikovi	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—	—	
P. notoensis	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	

GEOGRAPHICAL DISTRIBUTION (continued)

Species	Baltic Sea including the Skagerrak	North Sea	Norway Sea	Baffin Bay and Davis Strait	Greenland Sea and Polar Basin	Barents Sea	White Sea	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Bering Sea	Sea of Okhotsk	Sea of Japan	Yellow Sea	South China Sea	Northwest Pacific	Remarks
P. imajimai	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	California
Austrophyllum sphaerocephala	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	+	
Vitiazia dogieli	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Vitiaziphyllum nuchalum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Notophyllum foliosum	+	+	+	—	—	—	—	—	—	—	—	—	—	+	+	—	+	Northern parts of Atlantic and Pacific
N. imbricatum	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	+	Gulf of Alaska, Vancouver I., California, New Zealand
Nipponophyllum japonicum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Coast of Japan
N. sagamianum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Same
Eteone flava	+	+	+	+	+	+	—	+	—	—	+	+	+	+	—	—	—	Arctic-boreal species
E. longa	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	+	Same
E. delta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	Yangtse R.
E. spetsbergensis spetsbergensis	+	+	+	—	—	+	—	+	—	—	+	—	—	—	—	—	—	Mainly arctic species
E. spetsbergensis bistriata	—	—	—	—	—	—	—	—	—	—	+	+	+	+	—	—	—	
E. lactea	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	North Atlantic
E. vitiazi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Eteone (M.) ornata	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	
E. (Mysta) barbata	+	+	+	—	—	+	+	—	—	+	+	+	+	+	—	—	—	Arctic-boreal species
E. (M.) maculata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	—	
E. (M.) tchangsii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	—	? Coasts of India

GEOGRAPHICAL DISTRIBUTION (continued)

Species	Baltic Sea including the Skagerrak	North Sea	Norway Sea	Baffin Bay and Davis Strait	Greenland Sea and Polar Basin	Barents Sea	White Sea	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Bering Sea	Sea of Okhotsk	Sea of Japan	Yellow Sea	South China Sea	Northwest Pacific	Remarks
Lopadorhynchus appendiculatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	North Atlantic
L. brevis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific, Indian and Atlantic oceans
L. krohnii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
L. uncinatus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
Pelagobia longicirrata	—	—	+	+	+	—	—	—	+	—	—	—	+	—	—	—	+	Same
Maupasia caeca	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
M. brodskyi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Pedinosoma curtum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Northeastern Pacific, tropical and subtropical waters of Atlantic
Pontodora pelagica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific and Atlantic
Phalacrophorus pictus pictus	—	—	+	—	—	+	—	—	—	—	—	—	—	—	—	—	+	
Ph. pictus borealis	—	—	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	East coast of Greenland
Alciopidae																		
Torrea candida	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Atlantic Ocean, California
Naiades cantrainii	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
Vanadis formosa	—	—	+	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific, Indian and Atlantic oceans, mainly tropical and subtropical waters
V. longissima	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
Alciopa reynaudii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same

GEOGRAPHICAL DISTRIBUTION (continued)

Species	Baltic Sea including the Skagerrak	North Sea	Norway Sea	Baffin Bay and Davis Strait	Greenland Sea and Polar Basin	Barents Sea	White Sea	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Bering Sea	Sea of Okhotsk	Sea of Japan	Yellow Sea	South China Sea	Northwest Pacific	Remarks
Plotohelmis tenuis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific, Indian and Atlantic oceans, mainly tropical and subtropical waters
Alciopina parasitica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
Krohnia lepidota	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
K. excellata	—	—	—	—	—	—	—	—	—	—	—	+	—	—	—	—	+	Same
Rhynchonerella gracilis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Same
Rh. petersii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Tropical and subtropical waters of Pacific and Atlantic
Rh. angelini	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific, Indian and Atlantic oceans
Watelio gravieri	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	Pacific and Atlantic
Tomopteridae																		
Tomopteris septentrionalis	+	+	+	+	—	+	—	—	—	—	—	+	+	—	—	—		Same
T. elegans	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		Same
T. (Johnstonella) pacifica	—	—	—	—	—	—	—	—	—	—	—	+	+	—	—	—	+ + +	Northern parts of Pacific

GEOGRAPHICAL DISTRIBUTION (continued)

Species	Baltic Sea including the Skagerrak	North Sea	Norway Sea	Baffin Bay and Davis Strait	Greenland Sea and Polar Basin	Barents Sea	White Sea	Kara Sea	Laptev Sea	East Siberian Sea	Chukchi Sea	Bering Sea	Sea of Okhotsk	Sea of Japan	Yellow Sea	South China Sea	Northwest Pacific	Remarks
T. (J.) helgolandica	+	+	+	+	+	+	—	—	—	—	—	—	—	—	—	—	—	Northern parts of Atlantic
Typhloscolecidae																		
Typhloscolex muelleri	—	—	+	+	+	—	—	—	+	—	—	+	+	+	—	—	+	Cosmopolitan
Travisiopsis lobifera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Widely distributed, mainly in warm waters
T. levinseni	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	+	Widely distributed
T. lanceolata	—	—	+	+	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific and Atlantic
Sagitella kowalewskii	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	Pacific, Indian and Atlantic oceans
Lacydoniidae																		
Lacydonia papillata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	
Paralacydonia paradoxa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	Mediterranean, Indian Ocean

In the column "Remarks" only general data on distribution are given; more detailed data are to be found in the descriptions of the species.

92–95 *GLOSSARY OF IMPORTANT TERMS*

Abdomen — posterior modified part of the body of sedentary species, behind the thorax, sometimes ending in a special caudal appendage.

Abdominal, or **ventral cirrus** — cirrus on the ventral side of the parapodia.

Acicular setae, or **spine-shaped setae** — thick, simple setae, resembling acicula.

Aciculum (acicula) — axial internal seta supporting the branches of the parapodia; attached to the acicula are muscle fibers for retraction and projection of the external setae.

Anal cirri, or **urites** — situated on the margin of the anal lobe.

Anal lobe, or **pygidium** — posterior segment of the body, formed by the lower sphere of the trochophore; setae are never present on the anal lobe.

Axial seta — see Aciculum.

Biramous parapodium — parapodium divided into two branches (rami): a dorsal, or notopodium, and a ventral, or neuropodium, each with a bundle of setae.

Body segments — segments between the cephalic lobe and pygidium (see Metastomium).

Branchiae — appendages of varying form (cirriform, dendroid, etc.), mainly on the notopodia; branchiae in the form of simple bulging parts of the body wall are called coelomic branchiae, distinguished from brianchae with numerous branched capillaries.

Buccal, or **oral segment** — first segment after the cephalic lobe.

Caruncle — a sense organ in the form of a longitudinal ridge situated behind the cephalic lobe.

Cephalic lobe, or **prostomium** — first segment of the body, formed by the upper sphere of the trochophore.

Cephalic tentacles — tactile processes of the cephalic lobe.

Ceratophore — base of the cephalic tentacles.

Ceratostyle — distal part of the cephalic tentacles.

Chevron — chitinous plates on the proboscis of a Goniada, with a <<<<< arrangement.

Chromatophores — cells or groups of cells containing pigment.

Chromophile gland — densely arranged tubular gland cells on the ventral fins in the Tomopteridae.

Cirrate segments — segments with dorsal cirri (in contrast to scaly segments with dorsal scales — elytra).

Cirrophore — base of cirri.

Cirrostyle — elongate distal part of cirri.

Cirrus — tendril.

Complex seta (compound seta, soie composée) — consisting of two parts: a main shaft, or manubrium, and a distal part articulated with the manubrium.

Ctenidium — small processes of varying form on the cephalic lobe and on the parapodia; mainly sense organs.

Dorsal cirrus — cirrus on the upper (dorsal) side of the parapodia.

Dorsal scales, or **elytra** — dorsoventrally flattened dorsal cirri on some segments in the Aphroditidae; overlapping like tiles, covering a large part of the dorsal side of the body; they are frequently covered with chitinous papillae on the outer side.

Elytra — see Dorsal scales.

Elytrigerous segments — segments with dorsal scales, or elytra (in contrast to cirrate segments with dorsal cirri).

Elytrophore — base of the elytra, or dorsal scales.

Epaulettes — elongate processes behind the cephalic lobe (a form of nuchal organs).

Epitokial forms — sexually mature forms of varying form of benthic species which rise to the surface for spawning.

Felt — entangled, often silt-covered, thin, long notopodial setae covering the dorsal side of some Aphroditidae.

Fins — cutaneous fringes on the parapodia in the Tomopteridae.

Frontal cephalic tentacles — situated at the anterior margin of the cephalic lobe.

Frontal horns — pointed processes on the lobes of the cephalic lobe in some Aphroditidae.

Hairlike setae — simple, long, thin setae.

Heterogomph setae — complex (segmented) setae the main shaft of which bears two denticles of different size at the distal end.

Heteronereid stages — markedly modified sexually mature forms of Nereidae which surface for spawning.

Homogomph setae — complex (segmented) setae the main shaft of which bears two denticles of the same size at the distal end.

Hyaline glands — tubular glands on the fins of Tomopteridae.

Jaws — chitinous formations in the pharynx in the form of hooks and denticles.

Larval segments — developing simultaneously during metamorphosis of the trochophore, situated in the anterior part of the body.

Manubrium (shaft) of setae — main shaft of complex setae, forming the base of the distal part.

Marginal, or **oral**, **pharyngeal papillae** — surrounding the mouth.

Median, or **single cephalic tentacle** — situated on the dorsal side of the cephalic lobe, usually between the eyes (in the Phyllodocidae).

Metastomium — all segments of the body collectively.

Nectochete — last stage of planktonic larvae of polychaetes.

Nephropore, or **nephridial papilla** — opening of nephridia on the lower posterior side of the neuropodia.

Neuropodium — lower (ventral) branch of the parapodium.

Notopodium — upper (dorsal) branch of the parapodium.

Nuchal organs — depressions and processes covered with ciliated epithelium, at the posterior margin of the cephalic lobe; function apparently olfactory.

Occipital organ — see Nuchal organs.

Occipital papilla — a rounded papilla at the posterior end of the cephalic lobe.

Ommatophore — processes of the cephalic lobe, with eyes at the end.

Operculum — formations which cover the opening of tubes: in the Serpulidae, a branchial ray, in the Sabellariidae (Chermellidae), large golden setae arranged in a semicircle on the anterior part of the body.

Palea — large, strong, slightly flattened, golden setae on the anterior segments of the Ampharetidae, Pectinariidae and Sabellaridae, which form a fan or an operculum covering the external opening of the tube.

Palpod — a pointed process at the anterior end of the cephalic lobe in the Typhloscolecidae.

Palpophore — basal part of biarticulated palps.

Palpostyle — distal part of biarticulated palps.

Palps — paired appendages of the cephalic lobe, situated in the Errantia on the ventral side near the mouth (the coelomic cavity enters the palps).

Paragnathae — small, chitinous denticles in the pharynx in the Nereidae and Glyceridae.

Parapodia — lateral processes of segments, with setae and usually with dorsal and ventral cirri; function mainly locomotory.

Parapodial (podial) tongue — elongate, pointed parts of the noto- or neuropodia, above or below the podial lobe.

Parapodial trunk — elongate base of the parapodia before their division into noto- and neuropodium.

Peristomal, or **tentacular cirri** (cirri peristomales, cirri tentaculares) — tactile organs in the form of cirriform appendages on the modified anterior segments of the metastomium.

Peristomium — modified anterior segment formed by fusion of the oral segment with the following 1—3 segments.

Pharyngeal oral papillae — see Marginal pharyngeal papillae.

Pharynx — part of esophagus, usually strongly muscular, sometimes with chitinous jaws.

Podial lip — leaflike process of the podial lobe before (presetal) or behind (postsetal) the setae.

Podial lobe (setigerous lobe) — seta-bearing process.

Proboscis — eversible part of the pharynx.

Proboscis papillae — soft processes of varying type on the outer wall of the proboscis.

Proboscis sheath — anterior part of the esophagus which forms its external wall during eversion of the pharynx.

Prostomium — see Cephalic lobe.

Prototroch — ciliary belt at the anterior part of the trochophore.

Pseudobiramous (sesquiramous, sub-biramous) **parapodium** — a notopodium represented only by a dorsal cirrus, an aciculum, and sometimes by 1 or 2 hairlike setae.

Pygidium — see Anal lobe.

Receptaculum seminis — markedly expanded dorsal cirri on the anterior segments of female Alciopidae which form large pockets for keeping the spermatozoa.

Retort organ — a large gland opening into the buccal cavity in the Typhloscolecidae.

Rosette gland — dark glands on the parapodia of Tomopteridae — organs of luminescence.

Rostrum — distal widened part of the shaft of complex setae, usually ending in two articular denticles which support the distal part of the seta.

Scapha — markedly modified posterior segments of the Pectinariidae, forming a distinct caudal segment.

Setae — main armature of the parapodia; of different type (hairlike, flattened, hook-shaped, beaklike, spatulate, harpoonlike, hoelike, etc.); the main division is into complex (segmented) and simple setae.

Setae falcigerae — composite (segmented) setae with a distal part of sickle-shaped or hook-shaped form.

Setigerous sac (follicule setigérè) — epidermal depressions in the integument containing basal cells, which form the setae.

Simple seta — seta of varying form, consisting of a single part (see Complex seta).

Spinigerous setae — complex (segmented) setae with wedge-shaped distal part.

Spur glands — small glands on the ventral fins of the Tomopteridae, usually situated lateral to the chromophile glands.

Stomodeum — fore-intestine.

Stylodes — usually finger-shaped processes on the parapodia.

Telescopic eyes — large eyes with a lens in the Alciopidae.

Telotroch — a girdle of cilia in the posterior part of the trochophore.

Tentacular cirrus — see Peristomal cirri (tentacles).

Thoracic membrane — a thin cutaneous fringe surrounding the thoracic segments in the Serpulidae.

Thorax — anterior part of the body of sedentary species.

Tori (t. uncinigeri) — in the Sedentaria, ventral branches of the parapodia forming transverse ridges with a single row or several rows of hook-shaped setae (uncini).

Uniramous parapodium — parapodium with one podial lobe with a single bundle of setae.

Urites — see Anal cirri.

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Order **PHYLLODOCEMORPHA**

Suborder PHYLLODOCIFORMIA

This suborder contains the benthic forms with the simplest organization, the benthic Phyllodocidae and Lacydoniidae, and some highly specialized pelagic polychaetes, the planktonic Phyllodocidae, Alciopidae, Tomopteridae and Typhloscolecidae.

Cephalic lobe well developed and distinctly separated from the oral segment, fused to a greater or smaller extent with the anterior segments only in some pelagic forms. Cephalization in the earliest stages, a distinct peristomium absent. Cephalic lobe only with cephalic tentacles, palps absent. Pharynx tubular, partly eversible, forming a proboscis which is the main organ for the collection of food; chitinous jaws absent (present only in the pelagic genera Phalacrophorus and Pelagobia as two hooks at the anterior end of the proboscis).

All segments of the body strictly homonomous. Parapodia uniramous, rarely there is formation of the beginning stages of biramous parapodia. Bundle of setae on the parapodia not differentiated; variation of setae insignificant. Podial appendages simple, cirriform or leaf-shaped. Integument with ciliary epithelium in many places. Respiration takes place through the integument on the entire surface of the body, localized respiratory organs in the form of branchiae with branched capillaries absent. Circulatory system weakly developed, blood colorless, hemoglobin concentrated in the nervous system. Excretory system represented by protonephridia with solenocytes. Ventral nerve cord closely connected with the epithelial covering, in a primitive subepithelial position. Pelagic larvae, except for the usual provisional organs, without specialized adaptations. Mainly active predators. Benthic forms not building permanent shelters or tubes.

Key to families

1 (8). Segments of body with setae.
2 (7). Podial processes well developed, with numerous thin, long setae.
3 (6). Parapodia with a single bundle of setae.
4 (5). Cephalic lobe with a pair of large telescopic eyes. Pelagic species . . . . II. Family **Alciopidae** (p. 185)
111 5 (4). Cephalic lobe with small subepithelial eyes or without eyes. Mainly benthic species . . . . I. Family **Phyllodocidae** (p. 106)

6 (3). Parapodia with two separate bundles of setae (notopodium and neuropodium). Benthic species . . . . . . V. Family **Lacydoniidae** (p. 213)

7 (2). Podial processes reduced, with only 1–3 short, needlelike setae. Dorsal and ventral cirri broad, leaf-shaped. Pelagic species . . . . IV. Family **Typhloscolecidae** (p. 208)

8 (1). Segments of body without setae, podial processes only with a thin cutaneous fringe at the margin ("fins"). 2nd pair of tentacular cirri forming long "whiskers," directed slightly laterally and almost reaching the posterior end of the body. Pelagic species . . . . III. Family **Tomopteridae** (p. 201)

I. Family Phyllodocidae Oersted, 1843*

This family contains numerous benthic species of uniform organization; it also contains some pelagic forms, which show many aberrant characters.

The body of benthic Phyllodocidae is usually long and thin, distinctly dorsoventrally flattened, and usually consists of numerous segments of uniform structure. There may be over 700 segments in some species.

The Phyllodocidae are distinguished in life by their bright and variegated coloration. This is important systematically, but the color unfortunately fades after preservation in alcohol.

The cephalic lobe is well differentiated, conical, oval, rounded or heart-shaped, fused with the anterior segments only in pelagic forms. There are 2–5 cephalic tentacles on the cephalic lobe; palps absent. Eyes usually present (usually one pair, mainly at the posterior margin of the cephalic lobe).

Pharynx tubular; the everted anterior part of the pharynx forms a long proboscis which collects the food. The outer side of the proboscis is usually covered with numerous soft papillae, uniformly (diffusely) distributed or forming regular longitudinal rows; there are sometimes small chitinous spines; the aberrant pelagic genera Phalacrophorus and Pelagobia have 2 chitinous hooks at the anterior end of the proboscis, which are large in the first and small in the second genus (Figure 5, *12*, *13*).

On the first 2 or 3 circumoral ("peristomal") segments, which are reduc- 112 ed dorsally and partly fused, or distinctly demarcated, there 2–4 pairs of elongate tentacular cirri (they are usually filamentous or spindle-shaped). The other segments of the body, which are markedly wider than long, are of the same organization and differ little from each other. Parapodia in the form of an oblong podial lobe usually uniramous, i.e. with one aciculum and one bundle of setae, but in some genera (Austrophyllum, Notophyllum, Nipponophyllum), there is an additional notopodial aciculum and one or two small, hairlike setae; in this case, the parapodia are sometimes named biramous, but it is more correct to call them pseudobiramous, since the notopodial branch is only indicated, as there is only one podial lobe with

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* The name of the family is possibly taken from mythology, after Phyllodoce, a sea nymph, daughter of Nereus and Doris; sea nymphs, according to the legend, accompanied the Greek god Poseidon, called Neptune by the Romans. The literal translation "resembling leaves" well describes the appearance of polychaetes, since the dorsal cirri are flattened and leaflike; polychaetes are sometimes called "phyllopoda" ("leaf-legs").

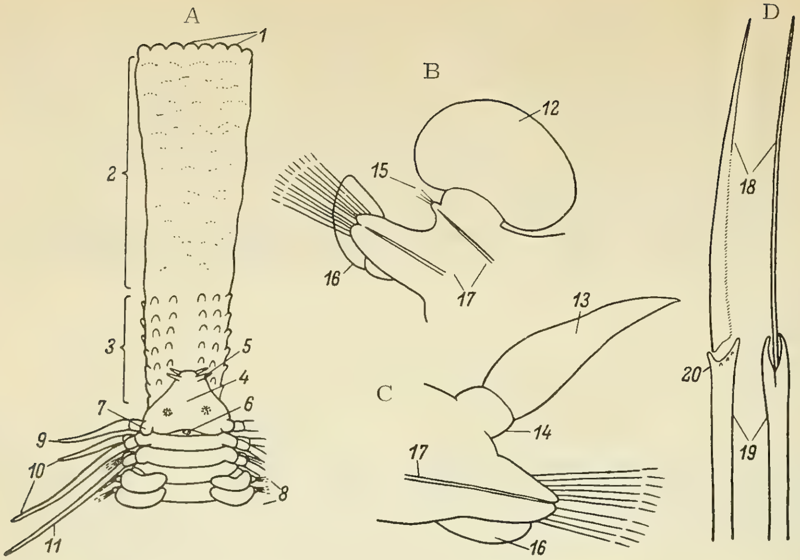

FIGURE 22. Terminology used in the description of Phyllodocidae:

A) cephalic end with everted pharynx; B) pseudobiramous parapodium; C) uniramous parapodium; D) complex, or segmented, seta, different aspects. 1 – marginal, or oral, papillae; 2 – distal part of proboscis with smooth or slightly rugose surface; 3 – proximal part of proboscis with regular longitudinal rows of conical papillae; 4 – cephalic lobe; 5 – paired cephalic tentacles; 6 – occipital nuchal papilla; 7 – lateral occipital organs; 8 – normal body segments; 9 – first pair of tentacular cirri on 1st segment; 10 – second and third pair of tentacular cirri on 2nd segment; 11 – fourth pair of tentacular cirri on 3rd segment; 12 – bean-shaped or kidney-shaped dorsal cirrus; 13 – lanceolate dorsal cirrus; 14 – cirrophore of dorsal cirrus; 15 – developing dorsal branch of parapodium (notopodium); 16 – ventral cirrus; 17 – aciculum; 18 – distal part of seta; 19 – shaft of seta; 20 – upper, slightly widened part of shaft with articular denticles (rostrum).

a single bundle of setae which form a fan. The parapodia of benthic forms usually bear leaf-shaped, relatively large dorsal cirri; they often overlap like tiles and cover part of the dorsal side, like the dorsal scales of the Aphroditidae. The podial lobe also bears a ventral cirrus, which is much smaller than the dorsal cirri. The dorsal and ventral cirri are often markedly reduced in pelagic species. The form of the podial cirri is important for the determination of species; it varies according to their position, and
113 on the anterior, middle and posterior segments the cirri may be distinctly different, so that comparison of the dorsal and ventral cirri should be made on the same part of the body. The dorsal cirri may be symmetrical or asymmetrical in relation to the cirrophore. The position of the main axis of the dorsal cirrus can be determined by the arrangement of the main nerve endings and gland cells. There are sometimes stripes of ciliary epithelium on the posterior side of the dorsal cirri (genus Phyllodoce, p. 123). There are two, usually long, anal cirri at the posterior end of the body.

The setae are long and thin and consist of two parts: the elongate shaft, or manubrium, which ends in a slightly widened rostrum, and the long, thin distal part, which is finely serrate on the inside and articulated with the shaft; such setae are called complex or segmented. There are simple rarely hook-shaped setae on the anterior segments (Lopadorhynchus, Chaetoparia).

The systematics of the Phyllodocidae is based at present on the structure of the anterior end of the body. The process of cephalization is in its first stages in the Phyllodocidae. The process extends only to the two anterior segments in some genera, but extends to some extent to the 3 anterior segments in others. The modified anterior segments may be distinctly separated from each other and from the cephalic lobe, but they are sometimes partly fused and reduced (Figure 2). A formula is used for the structure of the cephalic part, e.g. $(1 + S\frac{1}{1}) + S\frac{1}{N}$, explained on p. 64. The terminology used for the description of species is given in the legend to Figure 22.

The family Phyllodocidae, in my definition, contains about 40 genera and 275 species according to the catalogue of Hartman (1959, 1965a), but the systematic position of many species, and genera is still not clear. In the area dealt with in this work, species of 23 genera and 2 subgenera have been found.

Key to subfamilies, genera and subgenera of
the family Phyllodocidae sensu lato

1 (38). Benthic forms (subfamily Phyllodocinae Oersted).
2 (9). Two or only one anterior segment with tentacular cirri.
3 (6). Only one pair of tentacular cirri on 1st segment.
4 (5). Dorsal cirrus present on 3rd segment . . . . 1. Genus **Lugia** Quatrefages (p. 111)
5 (4). Dorsal cirrus on 3rd segment absent . . . . 2. Genus **Mystides** Theel (p. 113)
6 (3). Two pairs of tentacular cirri on 1st segment . . . . 17. Genus **Eteone** Savigny (p. 164)
7 (8). Proboscis smooth or tuberculate, with indistinctly defined, large, soft papillae on entire surface. Tentacular cirri short . . . . Subgenus **Eteone** Savigny s.str.
8 (7). Proboscis with 2 lateral longitudinal rows of large, soft papillae resembling the "lateral papillae"; rest of surface of proboscis with numerous small denticulate papillae. Tentacular cirri long . . . . Subgenus **Mysta** Malmgren
114 9 (2). Three anterior segments with tentacular cirri.
10 (37). Hook-shaped cirri setae absent on anterior segments.
11 (30). Special occipital processes (epaulettes) absent behind cephalic lobe.
12 (21). Cephalic lobe with 4 frontal tentacles (median dorsal tentacle absent).
13 (14). All first 3 segments separated and not reduced dorsally . . . . 3. Genus **Protomystides** Czerniavsky (p. 118)
14 (13). First 2 segments fused dorsally.
15 (16). Cephalic lobe oblong or rounded, without an occipital papilla . . . . 4. Genus **Genetyllis** Malmgren (p. 121)
16 (15). Occipital papilla present.

17 (20). Cephalic lobe heart-shaped; occipital papilla situated at posterior incision of cephalic lobe . . . . 5. Genus **Phyllodoce** Savigny s. lat. (p. 123)

18 (19). Papillae in basal part of proboscis diffusely distributed . . . . Subgenus **Phyllodoce** Savigny s. str.

19 (18). Papillae in basal part of proboscis arranged in longitudinal rows . . . . Subgenus **Anaitides** Czerniavsky

20 (17). Cephalic lobe rounded, with a long posterior process ("tongue") extending onto the 1st segment; occipital papilla situated at end of posterior process of cephalic lobe. . . . . 6. Genus **Paranaitis** Southern (p. 133)

21 (12). Cephalic lobe with 5 tentacles.

22 (29). Parapodia with one aciculum.

23 (26). All first 3 circumoral segments fully developed and distinct dorsally.

24 (25). All tentacular cirri of the same form (mainly cylindrical or spindle-shaped). . . . . 8. Genus **Eulalia** Savigny (p. 138)

25 (24). Lower tentacular cirri of 2nd segment flattened, with a posterior lateral fringe (swordlike), the others spindle-shaped . . . . 9. Genus **Steggoa** Bergström (p. 144)

26 (23). First circumoral segment reduced dorsally and fused with 2nd segment (first pair of tentacular cirri situated at posterior margin of cephalic lobe).

27 (28). All tentacular cirri of the same form: spindle-shaped, or slightly flattened . . . . 10. Genus **Eumida** Savigny (p. 145)

28 (27). Lower tentacular cirri on 2nd segment markedly flattened, with posterior lateral fringe (swordlike), the others spindle-shaped . . . . 11. Genus **Pterocirrus** Claparède (p. 151)

29 (22). Parapodia with 2 acicula . . . . 12. Genus **Austrophyllum** Bergström (p. 154)

30 (11). Occipital processes (epaulettes) behind cephalic lobe present.

31 (34). Parapodia with one aciculum.

32 (33). All 3 anterior segments fully developed . . . . 13. Genus **Vitiazia** Uschakov (p. 156)

33 (32). 1st segment reduced dorsally . . . . 14. Genus **Vitiaziphyllum** Uschakov (p. 158)

34 (31). Parapodia with 2 acicula (pseudobiramous).

35 (36). First one or two segments reduced dorsally . . . . 15. Genus **Notophyllum** Oersted (p. 159)

115 36 (35). First three segments reduced dorsally. . . . . 16. Genus **Nipponophyllum** Imajima and Hartman (p. 162).

37 (10). Setae on anterior segments simple, hook-shaped . . . . 7. Genus **Chaetoparia** Malmgren (p. 136).

38 (1). Pelagic forms.

39 (48). Parapodia well developed on all segments.

40 (41). Podial lobe elongate, like a long, thin fingerlike process (subfamily Pontodorinae Bergström). . . . 22. Genus **Pontodora** Greeff (p. 182)

41 (40). Podial lobe short (subfamily Lopadorhynchinae Claparède).

42 (45). Setae present at base of tentacular cirri.

43 (44). Two pairs of tentacular cirri on the same segment. Dorsal cirri absent on 2nd segment. Podial cirri very long, finger-shaped . . . . 19. Genus **Pelagobia** Greeff (p. 177)

44 (43). Three pairs of tentacular cirri on two segments. Podial cirri small
. . . . 20. Genus **Maupasia** Viguier (p. 179)
45 (42). Setae absent at base of tentacular cirri.
46 (47). Parapodia on all segments of the same type; only segmented setae
present . . . . 21. Genus **Pedinosoma** Reibisch (p. 181)
47 (46). Parapodia on first 2 or 3 segments of body markedly modified and
with large, simple, hook-shaped setae. . . . .
. . . . 18. Genus **Lopadorhynchus** Grube (p. 174)
48 (39). Parapodia on anterior segments greatly reduced (subfamily Iospilinae Bergström).
49 (50). Pharynx with two large chitinous hooks . . . .
. . . . 23. Genus **Phalacrophorus** Greeff (p. 183)
50 (49). Pharynx without chitinous hooks.
51 (52). To 11 anterior segments with reduced parapodia . . . .
. . . . ☆Genus **Iospilopsis** Augener, 1922
West Indies (Tortuga Island)
52 (51). Parapodia normally developed from the 5th segment onward.
53 (54). Dorsal and ventral cirri rudimentary on 2nd and 3rd segment . . . .
. . . . ☆Genus **Pariospilus** Viguier, 1911
Mediterranean
54 (53). Dorsal and ventral cirri absent on 2nd and 3rd segment . . . .
. . . . ★Genus **Iospilus** Viguier, 1866
Atlantic Ocean (Canary Islands, Madeira),
Mediterranean

Subfamily Phyllodocinae Oersted, 1843

(incl. Eteoninae Bergström, 1914; Lugiinae Bergström, 1914; Mystidinae Bergström, 1914; Protomystidinae Bergström, 1914)

Cephalic lobe large, usually distinctly separated from 1st segment. Four or five cephalic cirri. Two to four pairs of elongate tentacular cirri. Dorsal podial cirri on all body segments well developed; dorsal cirri larger than podial lobe. Anal lobe with 2 anal cirri. Body long, with a large number of segments (usually over 100). Benthic forms.

116 1. Genus LUGIA Quatrefages, 1865

Cephalic lobe oblong, slightly pointed, with 4 frontal tentacles; median tentacle and occipital nuchal papilla absent. Proboscis with soft papillae. First segment with one pair of elongate tentacular cirri, setae absent; 2nd segment with one pair of elongate dorsal, cylindrical cirri, podial lobes with setae and leaf-shaped cirri, which do not differ from the ventral cirri or are only slightly larger on the following segments; 3rd segment of normal structure. Formula of anterior segments: $1 + S\frac{1}{N} + S\frac{N}{N}$ or $1 + S\frac{1}{1} + S\frac{N}{N}$. Parapodia uniramous, setae segmented, with long, thin distal part. Small, thin worms.

Type species: Eteone pterophora Ehlers, 1864.

The genus Lugia is considered as one of the most primitive forms according to the structure of the anterior segments, from which could have developed the genera Mystides Théel and Protomystides Czerniavsky.

This genus was until recently thought to contain only the single species L. pterophora, which inhabits the Mediterranean; the worms live among coastal seaweeds; the second species of this genus, L. abyssicola, occurs in the northwestern Pacific Ocean, at a depth of over 5000 m. L. rarica (Ushakov, 1958a), from the Kuril-Kamchatka Trench, is now placed in the genus Mystides (see below).

Key to species of the genus Lugia Quatrefages

1 (2). One pair of eyes at posterior margin of cephalic lobe . . . . *L. **pterophora** (Ehlers, 1864)
Fauvel, 1923: 178–179, fig. 63, i.
Mediterranean
2 (1). Eyes absent . . . . 1. L. **abyssicola** Uschakov, n.sp.

1. **Lugia abyssicola** Uschakov n.sp. (Plate I, Figures 1–5)

Anterior part of cephalic lobe, with the frontal tentacles, separated from posterior part by a slight constriction; cephalic lobe indistinctly separated from 1st segment. Eyes absent. Proboscis densely covered with large, soft papillae, arranged in 6 more or less regular longitudinal rows. First segment with one pair of cylindrical, elongate tentacular cirri which are slightly widened at the base and pointed distally. Dorsal tentacular cirri on the 2nd segment of the same type as on the 1st, but slightly larger; ventral cirri oblong, leaf-shaped or oval, and almost twice as large as the ventral cirri on the following segments. The 3rd segment does not differ from the other segments of the body. Dorsal cirri on body segments oval, twice as long as broad, with rounded end; ventral cirri of the same form as the dorsal, but smaller; dorsal and ventral cirri with coarse alveolar structure. Podial
117 lobe bifid at the end, aciculum of light color. Setae in dorsal part of bundle with slightly serrate long, thin distal part, which is about half as long in the setae in the ventral part of the bundle. Anal cirri oval.

Specimens kept in alcohol are yellowish beige, without pigment spots. The type was taken from a lump of silt of red clay; the part of the body inside the tube was dark brown. Number of segments about 70. Length to 17 mm, width including parapodia 0.6 mm.

Type deposited at ZIN AN SSSR,* No. 1/15955.

Remarks. L. abyssicola closely resembles Mystides rarica (Uschakov) (p. 116) in its long cephalic lobe and the structure of the parapodia, but differs from it in the larger ventral cirri on the 2nd segment. The dorsal cirri of the 3rd segment, the presence or absence of which is of generic value (p. 113), may be lost during fixation; but in L. abyssicola and in most species of Mystides the dorsal cirri have no distinctly differentiated base and do not always leave distinct traces of attachment, so that it is often difficult to determine the genus of damaged specimens.

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* [Zoological Institute of the Academy of Sciences of the USSR.]

Distribution. Southeast of Hokkaido – 38°02' N and 146°33' E, depth 5475 m, ground: fine aleurite silt with an admixture of pumice pebbles ("Vityaz," station 3575, 7 May 1957 – type and 9 fragments); coast of California, south of San Francisco – 34°54' N and 123°56' W, depth 4200–4231 m ("Vityaz," station 4213, one specimen).

2. Genus **MYSTIDES** Théel, 1879 (emend. Hartmann-Schröder, 1963)

(incl. Mesomystides Czerniavsky, 1882; Pseudomystides, Bergström, 1914)

Cephalic lobe oblong, rounded, 4 frontal tentacles; median single cephalic tentacle and occipital nuchal papilla absent. One pair of eyes, sometimes absent. Proboscis with soft papillae. One pair of tentacular cirri on 1st segment, podial lobe and setae absent; dorsal tentacular cirrus present on 2nd segment, podial lobe with setae and with normal, often enlarged, ventral cirrus; dorsal cirrus absent on 3rd segment. All 3 anterior segments distinctly separated from each other and from the cephalic lobe. Formula: $1 + S\frac{1}{N} + S\frac{O}{N}$ or $1 + S\frac{1}{1} + S\frac{1}{1} + S\frac{O}{N}$. Parapodia uniramous. Setae segmented, but in mature forms (M. limbata S.-Joseph) there are also long, hairlike natatorial setae. Very small worms.

Type species: Mystides borealis Théel, 1879.

Théel (1879) did not state in his description whether the genus had dorsal cirri on the 3rd segment and this is also not shown in the figures. Southern (1914) again described M. borealis from the littoral of Ireland, and stated that dorsal cirri are absent on the 3rd segment. Bergström (1914) in his 118 monograph on the Phyllodocidae stated that dorsal cirri are present on the 3rd segment (!). Fauvel (1923), and Pettibone (1954, 1963), accepted Bergström's statement, and Pettibone shows dorsal cirri on the 3rd segment in the drawings of the anterior part of M. borealis. There is thus some confusion about M. borealis also about the description of the genus. Hartmann-Schröder (1963) reexamined the type specimen of Théel and established that a dorsal cirrus is absent on the 3rd segment of M. borealis. We examined a specimen of M. borealis from the Chukchi Sea (Point Barrow), received from Pettibone (Smithsonian Institution, Washington); it also has no dorsal cirri on the 3rd segment, although these are shown by Pettibone. In her revision, Hartmann-Schröder (1963) invalidated the subgenus Pseudomystides, which is characterized, like Mystides, by the absence of dorsal cirri on the 3rd segment. She had established in 1958 the new genus Hesionura (= Eteonides Hartmann-Schröder, 1960), which differs from Mystides only in the absence of setae on the 2nd segment. The above two genera are certainly closely related.

According to Hartmann-Schröder, the ventral cirrus on the 2nd segment of species of Mystides has become markedly modified; it is sometimes much enlarged and represents the 3rd pair of tentacular cirri, and sometimes only slightly modified compared with normal ventral cirri; there are thus in fact only 2 pairs of tentacular cirri, i.e. the formula is either $1 + S\frac{1}{1} + S\frac{O}{N}$ or $1 + S\frac{1}{N} + S\frac{O}{N}$. According to this interpretation of the genus Mystides, Lugia rarica Uschakov, 1958, described from the Kurile

Islands, which has a rounded ventral cirrus on the 2nd segment that differs little from the following ventral cirri, and no dorsal cirrus on the 3rd segment, has to be transferred to the genus Mystides. The distinctive character of this genus is the absence of dorsal cirri on the 3rd segment.

Hartmann-Schröder includes 4 species and one subspecies in the genus Mystides. She places M. caeca Langerhans, 1880 in the synonymy of M. borealis Théel, but we retain M. caeca as the subspecies M. borealis caeca (cf. Laubier, 1962). Hartmann-Schröder also includes in the synonymy of M. borealis, M. notialis Ehlers, 1913, and it is also difficult to agree with this. According to material from the Antarctic (Ushakov, 1962), we consider M. notialis as a valid species; it differs from M. borealis in the presence of simple setae on the posterior segments (which are absent in M. borealis). After the publication of Hartmann-Schröder's summary, Hartman (1965) described another subspecies, Pseudomystides limbata punctata, from New England and Bermuda, depth 200–4950 m, which, according to the above interpretation of the genus, should also be included in genus Mystides. I consider it as a distinct species. We found a new species, Mystides schroderae, in our material from the abyssal depths of the northwestern Pacific (see below).

119 Key to species of the genus Mystides Théel

1 (6). Cephalic tentacles longer than cephalic lobe. Tentacular cirri on 1st and 2nd segment longer than width of segment, distinctly widened at the base, with long, thin, threadlike ends (bottle-shaped).
2 (5). Simple setae absent.
3 (4). Eyes present . . . . 1. **M. borealis** Théel
4 (3). Eyes absent. . . . . ★**M. borealis caeca** Langerhans, 1880
Madeira, English Channel,
Mediterranean
5 (2). A single seta on the 2–5 posterior segments . . . .
. . . . ★**M. notialis** Ehlers, 1913
Littoral of Antarctic, Kerguelen,
Falkland Islands
6 (1). Cephalic tentacles shorter than cephalic lobe.
7 (16). Cephalic lobe longer than wide.
8 (11). Ventral cirri on 2nd segment small, resembling the ventral cirri on the other segments.
9 (10). Tentacular cirri on 1st segment spindle-shaped, long. . . . .
. . . . 2. **M. rarica** (Uschakov)
10 (9). Tentacular cirri on 1st segment leaf-shaped, short . . . .
. . . . ★**M. punctata** (Hartman, 1965)
New England and Bermuda,
depth 200–4950 m
11 (8). Ventral cirri on 2nd segment larger than the ventral cirri on the other segments.
12 (13). Ventral cirri on 2nd segment spindle-shaped, long, pointed. . . . .
. . . . 3. **M. schroderae** Uschakov
13 (12). Ventral cirri on 2nd segment leaf-shaped, flattened.

14 (15). Coloration of body uniformly brown; distal part of shaft of setae distinctly serrate . . . . ⋆**M. limbata limbata** Saint-Joseph, 1888
English Channel, littoral of Ireland, Mediterranean, Black Sea

15 (14). Median dark stripe on dorsal side of body distinct; distal part of shaft of setae weakly serrate . . . . ⋆**M. limbata nigrolineata** Rioja, 1925
Atlantic coast of Spain

16 (7). Cephalic lobe shorter than wide.

17 (18). Tentacular cirri distinctly shorter than width of segment; ventral tentacular cirrus on 2nd segment leaf-shaped . . . . 4. **M. southerni** Banse

18 (17). Tentacular cirri longer than width of segment; tentacular cirri on 2nd segment cylindrical . . . . ⋆**M. angolaensis** Augener, 1918
Littoral of West Africa (Angola)

120 1. **Mystides borealis** Théel, 1879 (Plate II, Figures 1–4)

Théel, 1879: 35–37, pl. II, figs. 29–32; Deryugin, 1915: 322; Zenkevich, 1925: 3; Augener, 1928: 711; Wesenberg-Lund, 1950b: 37; Pettibone, 1954: 232 (nec fig. 27, b); Khlebovich, 1961: 164–165; Pettibone, 1963: 74–75 (nec fig. 17, c); Hartmann-Schröder, 1963: 207–209 (synonymy, part.).

Cephalic lobe short, rounded. Cephalic tentacles thin, very long, threadlike, slightly longer than the cephalic lobe. Two large, dark eyes. Proboscis uniformly covered with small, soft, bottle-shaped papillae. Three pairs of tentacular cirri of about the same size: one pair on the 1st, two pairs on the 2nd segment. Tentacular cirri bottle-shaped, distinctly widened at the base, and with elongate, threadlike end. Dorsal cirri relatively small, thick, broadly oval or rounded; ventral cirri of the same form, slightly smaller than the dorsal cirri, projecting slightly beyond the podial lobe. Podial lobe slightly bifid at the end. Ten to 15 setae in a bundle; rostrum slightly widened and serrate; distal part elongate, pointed, sometimes slightly coiled or curved. Anal cirri large, oval.

Coloration yellowish brown, dorsal cirri dark, reddish brown. Number of segments 70–75. Small, delicate worms; length to 12 or 15 mm, width 1 mm.

Remarks. The illustration of M. borealis by Théel (1879) shows very small eyes, but the text states "large black eyes," so that the figure is apparently incorrect.

Our specimens from the Kuril Islands agree with the description of Southern (1914: 71–72, pl. VIII, fig. 17, A–D), except that eyes are absent in Southern's specimens. Fauvel (1923) thinks that the eyes have possibly faded, but Laubier (1962: 461) considers the specimens described by Southern as the subspecies M. borealis caeca Langerhans. We compared our specimens from the Kuril Islands with specimens from Point Barrow (Chukchi Sea) in the material of the Smithsonian Institution, and found them identical.

Deryugin (1915), Zenkevich (1925), Augener (1928) and Wesenberg-Lund (1950b) did not give a description, but we consider these specimens as typical M. borealis, since they were found in more or less the same region from which the type was described. M. borealis recorded by Prenant (1926) from Roscoff (Bretagne) certainly belongs to another genus, as it has a dorsal cirrus on the 3rd segment.

Distribution. Thirteen specimens from the Kuril Islands (littoral of Paramushir, Simushir and Shikotan, depth 30—100 m) in the ZIN collection. Isolated records from the Arctic coasts of Alaska, Novaya Zemlya, Spitsbergen, Kola Gulf, and on the west coast of Greenland have been published; according to Pettibone (1963), it is found from the Gulf of St. Lawrence to the Gulf of Maine. M. borealis caeca (Laubier, 1962) occurs off the coasts of Ireland and France, in the Mediterranean and near Madeira.

121 2. **Mystides rarica** (Uschakov, 1958) (Plate II, Figures 5—8)

Ushakov, 1958a: 204—205, fig., A—B (Lugia).

Cephalic lobe oblong, conical, slightly blunt anteriorly. Cephalic tentacles situated at end of cephalic lobe, much shorter than cephalic lobe. One pair of large eyes at sides of cephalic lobe near the posterior margin, situated deep beneath the epithelium (not always visible). One pair of long tentacular cirri on the 1st segment which are only slightly shorter than the width of the segment, spindle-shaped, tapering to a point. Dorsal tentacular cirri of the same form (spindle-shaped) on the 2nd segment as on the 1st segment, but slightly longer; ventral cirri short, flattened, rounded or slightly oblong, as large as or slightly larger than the ventral cirri on the other segments. Dorsal cirri oblong-oval on all following body segments (from the 4th), longer than wide; ventral cirri shorter than dorsal. Dorsal cirri much larger than the podial lobe, which is conical and bifid at the end. One aciculum of light color. Setae with long, fine and flexible distal part, 10—12 setae in a bundle; margin of distal part finely serrate; distal part of dorsal setae longer than on the ventral setae.

Coloration pale yellowish green, dorsal cirri slightly darker than the body. Many segments have small, dark spots at the base of the parapodia on the ventral side. To 95 segments. Length 15 mm, width (including parapodia) to 1 mm.

Remarks. In one specimen examined under the microscope, the retracted proboscis with large, soft papillae was clearly visible; it extended to the 30th segment.

Type deposited at ZIN, No. 1/1621.

Distribution. Kuril-Kamchatka Trench — 46°11' N and 154°56' E, depth 5070 m ("Vityaz," station 2119, type); same locality, depth 4850 m (station 2118, damaged specimen); south of Hokkaido — 39°44' N and 143°20' E, depth 1673—1748 m (station 3223, one specimen); near Bonin Island — 26°04' N and 141°56' E, depth 3305 m (station 3890, one specimen); northwest of Kermadek Island — 35°15' S and 172°14' E, depth 1125 m (station 3849, one specimen). New material shows that this species is widely distributed at great depths in the Pacific Ocean (it was possibly found at other abyssal stations, but the material is damaged).

3. **Mystides schroderae** Uschakov sp.nov. (Plate I, Figures 6–9)

Cephalic lobe oblong, slightly pointed, about twice as long as wide; anterior margin separated from other part of cephalic lobe by a slight constriction. Frontal tentacles short. Eye spots absent. Proboscis retracted (numerous soft papillae are visible under the microscope). All 3 pairs of tentacular cirri on the 2 anterior segments are long, cylindrical or spindle-shaped, pointed at the end; dorsal cirri on the 2nd segment the longest.
122 There is a small podial lobe with setae at the base of the tentacular cirri on the 2nd segment. Normal dorsal cirri beginning from the 4th segment; they are oblong-oval, larger than the podial lobe; ventral cirri of the same form, but much smaller. Setae not numerous (to 10 in a bundle), distal part very long in the dorsal setae, about 0.2 times as long in the ventral setae; margin of distal part serrate, articular denticles of rostrum with large spines. Anal cirri very long, pointed.

Coloration of body uniformly yellowish beige, darker at the base of the parapodia; anal cirri brown. Number of segments 103. Length 21 mm, width (including podial lobe) 0.5 mm.

Type deposited at ZIN, No. 1/16133.

This species has been named after Hartmann-Schröder, who published a revision of the genus Mystides. It differs from the abyssal species of this genus, which occur in the Atlantic, M. punctata (Hartman, 1967), and in the Pacific, M. rarica (Ushakov, 1958), mainly in the form of the tentacular cirri.

Distribution. Hawaiian Islands – 25°48' N and 174°12' W, depth 3095 m, light globigerina silt ("Vityaz," station 3781, type); east of Hokkaido – 37°38' N and 156°25' E, depth 5800 m ("Vityaz," station 3240, specimen without posterior end).

4. **Mystides southerni** Banse, 1954 (Plate III, Figures 1–6)

Banse, 1954 : 313–318, figs. 1–7; Sveshnikov, 1958 : 20, fig. 1; Hartmann-Schröder, 1963 : 213–214, figs. 15–17.

Cephalic lobe broad, slightly narrower anteriorly. Cephalic tentacles short (less than half as long as the cephalic lobe). Two large brown eyes near posterior margin of cephalic lobe. Tentacular cirri short (less than width of segment); ventral tentacular cirri on the 2nd segment the largest, slightly flattened and widened. Dorsal and ventral cirri oval. Shaft of setae at distal end with pointed denticles; distal part with oblique striation. Two thick, oblong-oval anal cirri.

To 20 segments. Length 1.6 mm.

Remarks. Mystides southerni Banse (1954), from Kiel Bay, is a benthic larval form which, as is typical for the genus Mystides (see above), has no dorsal cirri on the 3rd segment. Banse states that this larval form possibly belongs, together with Mystides sp. Thorson, 1946, to M. borealis Théel, sensu Southern, 1914 (nec Bergström, 1914), and proposes a new name to avoid confusion. The drawing of Mystides sp. in Thorson (1946) shows setae on the 1st segment, obviously a mistake. A juvenile Mystides was found by Sveshnikov (1958) in the White Sea, in rhizoids of Laminaria, and was identified as M. southerni, but the specimens of Sveshnikov and Thorson differ from that illustrated by Banse in having much longer tentacular cirri; these are possibly larval stages of distinct species.

Distribution. Kiel Bay, Kattegat, White Sea.

123 3. Genus **PROTOMYSTIDES** Czerniavsky, 1882

(emend. LaGreca, 1947; Hartmann-Schröder, 1962, 1963)

Cephalic lobe oblong or rounded, without posterior incision or occipital nuchal papilla, not always distinctly separated from the 1st segment, 4 frontal tentacles, median single tentacle absent. One pair of eyes, sometimes absent. Proboscis with soft papillae. Three or four pairs of tentacular cirri on the 3 anterior segments; all circumoral segments distinctly separated; setae present on all segments from the 2nd. Formula of anterior segments: $1 + S\frac{1}{N} + S\frac{1}{N}$ or $1 + S\frac{1}{1} + S\frac{1}{N}$. Parapodia uniramous (with one aciculum). Setae segmented, but simple natatorial setae may appear in mature specimens. Small worms.

Type species: Mystides bidentata Langerhans, 1880.

Hartmann-Schröder places in this genus some species in which the ventral cirrus on the 2nd segment differs distinctly from the ventral cirri on the other segments, but it is of normal form in the type species; I therefore give two formulas for the anterior segments, with 3 and 4 tentacular cirri. Ventral cirri on 2nd segment leaf-shaped, not cylindrical. Hartmann-Schröder (cf. also Day, 1960 : 306) thinks that the 1st segment may be fused with the cephalic lobe in some species of this genus; this extends the original diagnosis of this genus considerably. Species in which the 1st segment is fused dorsally with the cephalic lobe (e.g. Protomystides capensis Day, 1960) do not differ from species of Genetyllis Malmgren, 1865 (see below), because the 1st segment is also indistinguishable dorsally in Genetyllis, but it is apparently fused with the 2nd segment. A detailed anatomical examination is necessary in these cases.

According to Hartmann-Schröder, the genus Protomystides contains 7 species. I have now found a new species from abyssal depths near the Mariana Islands — Pr. orientalis Uschakov.

Key to species of the genus Protomystides Czerniavsky

1 (12). All 3 anterior segments separated from each other and from the cephalic lobe.
2 (3). Dorsal tentacular cirri of 3rd segment very long (extending to the 10th—11th segment). . . . . 2. **P. orientalis** Uschakov
3 (2). Dorsal tentacular cirri of 3rd segment short (extending to 5th—6th segment).
4 (5). Podial lobe very long . . . . 1. **P. levensteinae** Uschakov
5 (4). Podial lobe normal.
6 (7). Ventral tentacular cirri of 2nd segment not differing in size from ventral cirri of other segments. Cephalic lobe twice as long as

124 wide. . . . . ★P. bidentata (Langerhans, 1880)
English Channel, Mediterranean, Madeira, littoral of Brazil, New England, to a depth of 4950 m (Hartman, 1965)

7 (6). Ventral tentacular cirri of 2nd segment larger than of the following segments. Cephalic lobe short, shorter or only slightly longer than wide.

8 (9). Eyes absent. Articular denticles of rostrum of setae with numerous large spines. . . . . 3. **P. occidentalis** (Ditlevsen)

9 (8). Two eyes. Articular denticles of rostrum of setae with small spines.

10 (11). Cephalic lobe slightly longer than wide. Two dark, undulate lines from the 3rd segment at sides of dorsal surface . . . . ★P. **bilineata** La Greca, 1947
Mediterranean

11 (10). Cephalic lobe shorter than wide. Body uniformly covered with brown spots. . . . . ★ P. **brunnea** Hartmann-Schröder, 1963
Mediterranean

12 (1). First segment completely or partly fused with cephalic lobe.

13 (14). First segment completely fused with cephalic lobe. Dorsal cirri heart-shaped . . . . ★P. **capensis** Day, 1960
Western littoral of South Africa

14 (13). First segment partly fused with cephalic lobe.

15 (16). Dorsal cirri oval . . . . ★P. **confusa** Hartmann-Schröder, 1962
Littoral of Peru

16 (15). Dorsal cirri lanceolate . . ★P. **lanceolata** Hartmann-Schröder, 1962
Littoral of Peru

1. **Protomystides levensteinae** n.sp. (Plate I, Figures 10–12)

Cephalic lobe conical, longer than wide. Frontal tentacles short. Eyes absent. Proboscis in type specimen long, dark brown to the 11th segment. All 3 anterior segments distinctly separated from each other and from the cephalic lobe, about as long as the other body segments. One pair of cylindrical tentacular cirri on 1st segment, slightly longer than half the width of the segment. Dorsal tentacular cirri of 2nd segment lost, but traces of their attachment are clearly visible. Podial lobes on 2nd segment relatively short, with long setae, ventral cirri flat and rounded, much larger than on all other segments. Dorsal tentacular cirri of 3rd segment cylindrical, about as long 125 as 3 segments, longer than the first pair of tentacular cirri. Dorsal cirri of most body segments lost; they are long, distinctly longer than the podial lobe on the 6th and 11th segment, but they are shorter than the podial lobe on the middle and posterior segments (Plate I, Figure 11). Podial lobe elongated on all body segments. Ventral cirri on body segments small, rounded. Dorsal and ventral cirri with coarse alveolate structure. Setae very long and thin, their distal part longer than the shaft; to 10 setae in a bundle, some simple, long, hairlike setae between them (to 2 in a bundle); length of setae to 0.7 mm. Articular denticles of complex setae with small spines, distal part serrate. Anal cirri lost.

About 115 segments. Length 13 mm, width without parapodia 0.2 mm; podial lobes 0.1 mm long. Coloration uniformly yellowish beige; dark part of proboscis visible through anterior part of body.

The above description is based on the type. The species is named after R. Ya. Levenshtein (Institute of Oceanology, Academy of Sciences of the USSR), who worked on abyssal polychaetes collected by the "Vityaz."

Three specimens deposited at ZIN, No. 1/16138.

Remarks. In addition to the type, the ZIN collection contains 2 specimens from the Aleutian Islands which closely resemble the type, but their dorsal cirri are more elongate, and the setae are shorter; in one specimen, the ventral tentacular cirri of the 2nd segment were more elongate. One specimen from station 4066 had an everted pharynx; proboscis densely covered with flat, rounded, granulate papillae. The species differs from all other species in the very long podial lobes.

Distribution. Mariana Islands – 15°04' N and 141°50' E, depth 4549 m ("Vityaz," station 3900 – type); North Pacific, south of the Aleutians – 47°19' N and 175°49' W, depth 5681–5740 m ("Vityaz," station 4066, 2 specimens).

2. **Protomystides orientalis** Uschakov, n. sp. (Plate II, Figures 9–12)

Cephalic lobe rounded, strongly pigmented, with a distinct dark median stripe. Frontal cirri thick, short, with pointed end. Eyes absent. Proboscis retracted (not examined). All 3 anterior segments distinctly separated from each other and from the cephalic lobe. All tentacular cirri spindle-shaped, elongate; cirrus of 1st segment reaching the 6th segment, cirrus of 3rd segment reaching the 10th or 11th segment. Podial lobe of 2nd segment with setae. Dorsal cirri of body segments oblong; they are shorter and broader on the anterior segments than on the middle segments; podial lobe relatively small; ventral cirri elongate, slightly pointed, projecting beyond the podial lobe. Dorsal and ventral cirri with coarsely alveolate structure. Setae with long, thin distal part, which may be coiled; articular denticles with large spines. Anal lobe transverse-oval, anal cirri oblong-oval.

126 The worm was in a thin sandy tube.

Coloration of cephalic lobe and lateral parts of dorsal side brownish, with a dorsal median line, head and podial appendages of lighter color. To 110 segments. Length 13 mm, width 1 mm.

Type deposited at ZIN, No. 1/16448.

A specimen from New Zealand with eggs in the parapodia (eggs 0.012 mm).

This species differs distinctly from all other species of the genus in its very long tentacular cirri (such long cirri are characteristic for the genus Phyllodoce).

Distribution. East of Honshu – 38°36' N and 142°12' E, depth 598 m ("Vityaz," station 3597, type); near northern part of New Zealand, depth 1225 m ("Vityaz," station 3840, one specimen).

3. **Protomystides occidentalis** (Ditlevsen, 1917) (Plate III, Figures 7–9)

Ditlevsen, 1917: 62, pl. IV, figs. 8, 11, 15 (Mystides); Wesenberg-Lund, 1950a: 11, 1950b: 37 (Mystides); Hartmann-Schröder, 1963: 233–234, figs. 48–50.

Cephalic lobe semicircular, as long as wide. Frontal tentacles short. Eyes absent. Proboscis not examined. All 3 peristomal segments clearly separated from each other and from the cephalic lobe. First segment with one pair of tentacular cirri, which are about half as long as the width of the segment. Second segment with 2 pairs of tentacular cirri, dorsal cirri slightly longer than the ventral, between a podial lobe with setae. One pair of dorsal cirri on the 3rd segment, which are slightly longer than on the 2nd segment; podial lobe with setae and ventral cirrus. Tentacular cirri not longer than 3 segments. Dorsal cirri of body segments oblong-oval, slightly longer than the podial lobes; ventral cirri slightly shorter than the podial lobes. Anterior lip of podial lobe bilobed. Parapodia with 11–15 setae. Articular denticles of rostrum of setae with numerous small spines and 4 or 5 long spines; distal part serrate, with oblique striation; there are also one or two setae with a very short distal part.

Number of segments 160 (specimen incomplete), length 36 mm.

The type was reexamined by Hartmann-Schröder (1963). Not found in collections of ZIN.

Distribution. Known only from Davis Strait, depth 580 m.

4. Genus **GENETYLLIS** Malmgren, 1865

(Carobia Quatrefages, 1865)

Cephalic lobe rounded, without occipital nuchal papilla. Four frontal tentacles; median single tentacle absent. Two eyes. Proboscis with soft, diffusely distributed papillae. Four pairs of tentacular cirri on 3 anterior segments; 1st segment separated from cephalic lobe, but 1st and 2nd
127 segment fused and markedly reduced dorsally; 3rd segment normally developed; setae present from 2nd segment. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. Parapodia uniramous (with one aciculum); all setae segmented.

Type species: Genetyllis lutes Malmgren, 1865.

The genus Genetyllis Malmgren is closely related to Nereiphylla Blainville, 1828, differing from it only in that the tentacular cirri are all spindle-shaped, while some of them are slightly flattened in Nereiphylla; however, this is hardly a reason for separating the two genera.

This genus contains about 10 species. There are 2 species in our collection, Genetyllis lutea Malmgren and G. castanea (Marenzeller).

Key to species of the genus Genetyllis Malmgren

1 (2). Dorsal cirri shorter than wide . . . . 1. **G. lutea** Malmgren
2 (1). Dorsal cirri as long as or longer than wide . . . . 2. **G. castanea** (Marenzeller)

1. **Genetyllis lutea** Malmgren, 1865 (Plate III, Figures 10–12)

Malmgren, 1865: 93–94, pl. XIV, 32 (the cephalic lobe has been shown by mistake with 5 cephalic tentacles in the text and drawing; this was corrected by the author in 1867); McIntosh, 1908 : 95–96, pl. LXVIII, figs. 18–19; 1910 : pl. LXXVII, fig. 13; Bergström, 1914 : 160–161, textfig. 54, pl. 1, figs. 2–3 (synonymy); Eliason, 1920 : 25; Wesenberg-Lund, 1951 : 25–26.

Cephalic tentacles thick, massive, with sharply pointed ends. Two large, black eyes. Ventral tentacular cirri of 2nd segment markedly flattened. Dorsal cirri on body segments broad, slightly reticulate, with a deep incision at the base; dorsal cirri wider than long. Podial lobe oblong-conical, slightly bifid at the end. Ventral cirri oval, with a deep incision at the base. Rostrum of setae with small spines, distal part finely serrate.

Coloration uniformly orange-brown, well preserved in alcohol. To 180 segments. Length to 40 mm, width including the parapodia 3–4 mm.

Distribution. Kattegat, Skagerrak, coasts of Norway, Iceland and Scotland. One specimen in the ZIN collection from the Kattegat, depth 43 m, on sand (coll. Eliason).

2. **Genetyllis castanea** (Marenzeller, 1879)

Marenzeller, 1879 : 19–20, pl. III, fig. 2 (Carobia); Moore, 1909a : 239–240; 1909b : 339 (Phyllodoce (Carobia)); Izuka, 1912 : 199–200, pl. XXI, fig. 3 (Carobia); Bergström, 1914 : 158–160, fig. 53; Fauvel, 1919 : 359–360 (Phyllodoce) (synonymy); 1932 : 68 (Phyllodoce); 1933 : 15 (Phyllodoce); 1936 : 56–57 (Phyllodoce); Okuda, 1938 : 88 (Phyllodoce); Hartman, 1944 : 247; Berkeley and Berkeley, 1948 : 44–45 (Phyllodoce
128 (Genetyllis)); Ushakov, 1950 : 170, pl. 1, fig. 4 (Phyllodoce (Genetyllis)); 1955a : 93, fig. 2, D, E (Phyllodoce (Nereiphylla)); Khlebovich, 1961 : 161–162 (Phyllodoce (Nereiphylla)); Imajima and Hartman, 1964 : 65; Ushakov and Wu Pao-ling, 1965 : 150–151 (Phyllodoce (Nereiphylla)); Buzhinskaya, 1967 : 79 (Phyllodoce (Nereiphylla)); Imajima, 1967 : 410.

Cephalic tentacles large, spindle-shaped, sometimes longer than the cephalic lobe. Two large, rounded or slightly oblong black eyes. Sometimes a slight depression at the posterior margin of the cephalic lobe. Tentacular cirri slightly flattened, pointed distally; dorsal cirri on 2nd segment the longest, reaching the 6th segment. Dorsal cirri slightly asymmetrical, heart-shaped, with pointed end, as long as or longer than wide; the dorsal cirri completely cover the dorsal side in the anterior part of the body. Podial lobe short, with two small, rounded lips. Ventral cirri oval, larger than the podial lobe. Anal cirri thick, 3 or 4 times longer than wide. Rostrum of setae with small spines at the distal end; distal part finely serrate.

Coloration of body and appendages dark red or orange-brown; yellowish transverse stripes on the dorsal side, sometimes with a greenish tinge. Number of segments 150 or 200. Length to 40 mm, width including the parapodia to 3 mm.

Distribution. Sea of Okhotsk, Yellow Sea, South China Sea, Sea of Japan, mainly from shallow water, but to a depth of 500 m in the Sea of Okhotsk (about 40 specimens). Widely distributed, mainly in subtropical and tropical regions: littoral of Japan, India, Ceylon, California, Australia, New Zealand; Persian Gulf, Red Sea, Galapagos Islands.

5. Genus **PHYLLODOCE** Savigny, 1818, sensu lato

(incl. Anaitides Czerniavsky, 1882)

Cephalic lobe heart-shaped, with an occipital incision in which is situated a small occipital tubercle, the nuchal papilla. Four small tentacles at anterior end of cephalic lobe. One pair of large eyes. A pair of retractile nuchal processes behind the cephalic lobe. Proboscis cylindrical or hexahedral; its anterior part usually smooth or distinctly tuberculate, sometimes with irregularly distributed papillae; its posterior part with numerous soft, oblong or conical papillae, arranged in regular longitudinal rows (subgenus Anaitides) or diffusely distributed (subgenus Phyllodoce sensu stricto); 16–20 large, rounded marginal (terminal) papillae at the outer margin of the proboscis. First segment partly reduced dorsally and indistinct. Four pairs of cylindrical (spindle-shaped) or slightly flattened, long tentacular cirri on the first 3 segments. First pair of tentacular cirri, apparently situated below and lateral to the cephalic lobe in dorsal view, because it partly covers the strongly reduced 1st segment. The dorsal tentacular cirri on the 2nd 129 and 3rd segment are the longest. Setae on 2nd and 3rd segment present in some, absent in other species of the genus. Formula of anterior segments: $(1)\ S\frac{1}{1}) + S\frac{1}{N}$, $(1 + O\frac{1}{1}) + S\frac{1}{N}$ or $(1 + O\frac{1}{1}) + O\frac{1}{N}$.

Parapodia uniramous (with one aciculum). The dorsal cirri on the body have a distinct ciliary stripe on the dorsal margin of the posterior side; this stripe forms a kind of membrane (particularly well visible in large specimens of Ph. groenlandica). Setae numerous, all segmented; rostrum of shaft of setae slightly widened and bearing small spines; distal part elongate, saberlike, finely serrate on the slightly concave side.

Type species: Nereis maculata Linné, 1767.

Some authors (Hartman, 1959, and others) consider Anaitides Czerniavsky as a distinct genus. The main difference between Anaitides and Phyllodoce sensu stricto is the arrangement of the papillae on the proximal part of the pharynx. However, the arrangement of the papillae in the lower part of the pharynx is very variable in Anaitides variabilis Hartmann-Schröder, 1965 (there are sometimes longitudinal rows of papillae and sometimes the papillae are arranged diffusely). Hartmann-Schröder proposes an additional character for the definition of these genera: setae are present on the 2nd and 3rd segment in Phyllodoce sensu stricto, but they are absent on these two segments, or only on the 2nd segment, in Anaitides. This character, however, is not reliable, as there are no setae on the 2nd and 3rd segment in Ph. malmgreni Gravier, but the papillae on the lower part of the pharynx are diffusely distributed. Anaitides is best considered as a subgenus of Phyllodoce.

Hartman (1966 : 187) described a new genus, Prophyllodoce, which differs from Phyllodoce Sav. only in the presence of an additional pair of small tentacular cirri on the 1st segment; she gives the following formula of the anterior segments of Prophyllodoce: $\frac{1}{1} + \frac{1}{1} + \frac{1}{N} + S\frac{N}{N}$. However, the additional pair of "tentacular cirri" on the 1st segment are, in our opinion, projecting nuchal organs, observed in some species of the genus Phyllodoce, and we therefore think that the establishment of the genus Prophyllodoce is justified.

The genus Phyllodoce contains over 50 species, but many of them are incompletely described and their systematic position is doubtful. In the western part of the Baltic Sea are found Ph.(A.) mucosa Oerst. and Ph.(A.) maculata (L.), in the Polar Basin and in the Far East, Ph.(A.) maculata (L.), Ph.(A.) groenlandica Oerst., Ph.(A.) citrina Mgrn., in the Sea of Japan also Ph. laminosa brevis Zachs; in the Yellow Sea Ph. gracilis Kinberg, Ph.(A.) chinensis Uschakov and Wu and Ph.(A.) papillosa Uschakov and Wu; in the East China and South China seas, Ph. laminosa Sav., Ph. malmgreni Gravier, Ph.(A.) madeirensis Lang and Ph.(A.) papillosa Uschakov and Wu. Imajima and Hartman (1964); Imajima (1967) record from the littoral of Japan Ph. macrolepidota Schmarda, Ph. violacea Treadwell (? = Ph. pruvoti Fauvel), Ph. japonica Imajima, and Ph.(A.) elongata Imajima, but these species are not represented in our collection.

130 Key to subgenera and species of the genus Phyllodoce Savigny, sensu lato

1 (8). Basal (proximal) part of proboscis with numerous diffusely arranged papillae (subgenus Phyllodoce sensu stricto Savigny).
2 (7). Setae present on 2nd and 3rd segment.
3 (6). Dorsal cirri asymmetrical or heart-shaped.
4 (5). Dorsal cirri in middle of body asymmetrical, slightly longer than wide. . . . . 1a. **Ph.** (s. str.) **laminosa laminosa** Savigny
5 (4). Dorsal cirri in middle of body symmetrical (heart-shaped), wider than long. . . . . 1b. **Ph.** (s. str.) **laminosa brevis** Zachs
6 (3). Dorsal cirri lanceolate . . . . . . 2. **Ph.** (s. str.) **gracilis** Kinberg
7 (2). Setae absent on 2nd and 3rd segment. Dorsal cirri irregularly rhomboidal . . . . 3. **Ph.** (s. str.) **malmgreni** Gravier
8 (1). Papillae forming regular lateral, longitudinal rows on proximal part of proboscis (subgenus Anaitides Czerniavsky).
9 (10). Basal part of proboscis with 8 longitudinal rows of papillae (4 rows on each side); 3–6 papillae in a row. Dorsal cirri extending onto the dorsal side of the body . . . 7. **Ph. (Anaitides) citrina** Malmgren
10 (9). Basal part of proboscis with 12 longitudinal rows of papillae.
11 (12). Distal part of proboscis with large teat-shaped papillae . . . . 10. **Ph. (Anaitides) papillosa** Uschakov and Wu
12 (11). Distal part of proboscis smooth or tuberculate (without teat-shaped papillae).
13 (18). Setae present on 3rd segment.
14 (17). Dorsal cirri extending slightly onto dorsal side.
15 (16). Ventral cirri elongate, pointed . . . . 6. **Ph. (Anaitides) mucosa** Oersted
16 (15). Ventral cirri short, rounded . . . 5. **Ph. (Anaitides) maculata** (L.)
17 (14). Dorsal cirri extending distinctly onto dorsal side. . . . . 4. **Ph. (Anaitides) groenlandica** Oersted
18 (13). Setae absent on 3rd segment.
19 (20). Dorsal cirri broadly oval or bean-shaped . . . . 8. **Ph. (Anaitides) chinensis** Uschakov and Wu
20 (19). Dorsal cirri elongate, pointed . . . . 9. **Ph. (Anaitides) madeirensis** Langerhans

Subgenus PHYLLODOCE Savigny, 1818, sensu stricto

Papillae diffusely distributed in basal part of proboscis.

1a. **Phyllodoce** (s. str.) **laminosa laminosa** Savigny, 1818

Bergström, 1914 : 150–152, fig. 48 (synonymy); Fauvel, 1923 : 145–146, fig. 51, a–e; 1939 : 274–275.

Cephalic lobe with a large posterior heart-shaped incision and an occipital papilla. Anterior part of proboscis hexahedral, transversely wrinkled,
131 with 16–20 marginal rounded papillae; proximal part with numerous soft,
pointed, diffusely distributed papillae. Tentacular cirri extending posteriorly to the 14th to 18th setigerous segment. Setae present on 2nd and 3rd segment. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$.

Dorsal cirri large, oblong-oval anteriorly, irregularly heart-shaped, asymmetrical in middle of body, longer than wide. Ventral cirri elongate, projecting beyond the end of the podial lobe; they are blunt anteriorly, more pointed in the middle of the body.

Dorsal side bluish slate, iridescent, with transverse greenish and brownish spots; dorsal cirri olive greenish, brownish green or brownish red if preserved in alcohol. Several hundred segments. Length to 150–750 mm (Fauvel, 1923).

Remarks. Ph. laminosa Savigny has been recorded from the southwestern part of the Barents Sea (Zatsepin, 1948 : 111–112), but this needs confirmation. A specimen from the Mediterranean is in the ZIN collection.

Distribution. North Sea, Atlantic coast of Europe, Mediterranean, littoral of Indo-China (Fauvel, 1939).

1b. **Phyllodoce** (sensu stricto) **laminosa brevis** Zachs, 1933

Zachs, 1933 : 127; Annenkova, 1938 : 141; Ushakov, 1955a : 91.

Differs from Ph. laminosa laminosa Savigny in the shorter and more symmetrical dorsal cirri, which are shorter than wide, and in the shorter body. Number of segments to 15. Length to 40 mm, width to 3.5 mm (Zachs, 1933).

Not represented in the ZIN collection.

Distribution. Peter the Great Bay in the Sea of Japan.

2. ? **Phyllodoce** (sensu stricto) **gracilis** Kinberg, 1866

Kinberg (1866) 1910 : 55, pl. XXII, fig. 3, A, G; (nec Verrill, 1873; Fauvel, 1932 : 69, textfig. 12; ? Monro, 1939 : 173–175, fig. 3; Hartman, 1948b : 49, pl. VII, figs. 4–6 (Genetyllis); Fauvel, 1953 : 117, fig. 57; Ushakov and Wu Pao-ling, 1962a : 123–124; 1965 : 149–150.

Cephalic lobe rounded, with a slight posterior depression. Two large, dark eyes. Pharynx of our specimen retracted and not examined. Two anterior segments fused dorsally. The longest tentacular cirri reach the 9th segment. Setae present on 2nd segment. Formula: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. Dorsal cirri situated on high cirrophores, small and elongate (lanceolate), longer than wide. Ventral cirrus longer than podial lobe, with long, pointed end.

Cephalic lobe, dorsal cirri and entire surface of body densely covered dorsally and ventrally with distinct, slightly oblong, dark brown spots which are of more intense color on the anterior segments, the cephalic lobe and the dorsal cirri, so that the dorsal cirri appear dark brown; a small white spot in the form of a depression at the posterior end of the cephalic lobe 132 where the occipital papilla is usually situated. About 35 segments. Length about 5 mm, width 0.5 mm.

The above specimen from the Yellow Sea (T'ang-ku) is deposited in the Institute of Oceanology of the Academy of Sciences, Republic of China (Tsingtao).

Remarks. The type of Ph. gracilis Kinberg was reexamined by Hartman (1948b: 49), who placed it in the genus Genetyllis Malmgren because the 1st and 2nd segment are fused and reduced dorsally. But as Hartman also stated that there is a nuchal papilla, this species has to be placed in the genus Phyllodoce Sav. According to Hartman, the basal part of the proboscis is diffusely covered with numerous papillae (see also Kinberg's drawing).

Monro (1939) recorded this species from the Marquesas and Tahiti, but he did not find setae on the 2nd segment in his specimens. Fauvel (1932), however, stated that setae were present on the 2nd segment in his specimen, which was obtained from the Andaman Islands; this is also the case in our specimen, but as the dorsal cirri are shorter than in the specimen described by Fauvel, a question mark is added.

Hartman (1959) places Ph. ovalifera Augener, 1913, from the littoral of Southwest Australia, in the synonymy of this species and Monro (1939) Ph. fakaravana Chamberlin, 1919, from the Tuamotu Islands.

Distribution. Tropics — Bay of Bengal (Andaman Is.), Polynesia, possibly Australia.

3. **Phyllodoce** (sensu stricto) **malmgreni** Gravier, 1900 (Plate IV, Figures 4—6)

Gravier, 1900 : 207—209, pl. X, figs. 29—31, textfigs. 66—69; Fauvel, 1919 : 360—361; Augener, 1927b : 130—131; Monro, 1931 : 9; Fauvel, 1932 : 68—69; Monro, 1934 : 360; Fauvel, 1953 : 117, fig. 56, h; Day, 1957 : 68; Rullier, 1965b : 172—174, fig. 3; Day, 1967 : 147, fig. 5, 2, n—p.

Cephalic lobe with a small posterior incision, occipital nuchal papilla indistinct. Eyes with small lenses. Proximal part of proboscis with numerous diffusely distributed papillae (not forming regular longitudinal rows); distal part with 6 broad longitudinal tuberculate ridges (hexahedral). Dorsal tentacular cirri on 2nd and 3rd segment spindle-shaped, long, if drawn posteriorly, they reach the 15th segment; tentacular cirri of 1st segment and ventral tentacular cirri of 2nd segment shorter and more flattened. Setae absent on 2nd and 3rd segment. Formula: $(1 + O\frac{1}{1}) + O\frac{1}{N}$.

Dorsal cirri irregularly rhomboidal, longer than wide; dorsal cirri with large, oblong gland cells. Ventral cirri pointed, extending beyond the podial lobe. Rostrum of setae with small, pointed spines; distal part with distinct, oblique, fine striation.

Dark transverse spots in the median line of the dorsal side of the segments which form a longitudinal dark stripe in the anterior part of the body; dorsal cirri with weak brown pigmentation in the middle; in a female with numerous large eggs in the body cavity and in the parapodia (8 July 1961), the
133 pigmentation was diffuse. Two hundred or more segments. Body long and thin. Length 60–70 mm, width 1–2 mm.

Remarks. Our specimens do not differ from Ph. malmgreni Gravier, 1900 from Djibouti (Red Sea) (coll. Fauvel). Day (1967) states that there are setae on the 3rd segment in his specimens from the littoral of Mozambique, but setae are absent on the 3rd segment in the specimens of Fauvel and Rullier and also in our specimens. According to Hartman (1959: 162), Ph. malmgreni Gravier, 1900 is closely related to Ph. novaehollandiae Kinberg, 1866 from the littoral of Southeast Australia.

Distribution. Five specimens from Hainan Island (Hoihow, middle horizon of silty beach, pool with young Limulus) and from the Gulf of Tonkin, depth 28–53 m, are in the ZIN collection. According to the literature: Red Sea, Madagascar, Mozambique, East China Sea (Amon), New Guinea, coast of East Australia.

Subgenus ANAITIDES Czerniavsky, 1882

Papillae forming longitudinal rows on basal part of proboscis.

4. **Phyllodoce (Anaitides) groenlandica** Oersted, 1842 (Plate V, Figures 1–4)

Malmgren, 1867: 21, pl. II, fig. 9; 22, pl. II, fig. 10 (Ph. luetkeni); Théel, 1879: 34–35; Hansen, 1882: 31, pl. III, figs. 21–23 (Ph. arctica); McIntosh, 1908: 86–88, pl. LVIII, fig. 5, pl. LXVIII, figs. 4–6, pl. LXXVIII, fig. 7 (synonymy); ? Izuka, 1912: 198–199, pl. XXI, fig. 2; Bergström, 1914: 141–143, fig. 12 (Anaitides); Ditlevsen, 1917: 56; Fauvel, 1923: 153–154, fig. 54, f–i; Augener, 1928: 703–705 (synonymy); Deryugin, 1928: 239; Annenkova, 1932a: 167; 1937: 156; Gorbunov, 1946: 38; Zatsepin, 1948: 111, pl. XXIX, fig. 2, b–d (Anaitides); Hartman, 1948a: 19 (Anaitides); Berkeley and Berkeley, 1948: 46, fig. 66; Ushakov, 1948a: 27; 1950: 170; Wesenberg-Lund, 1950a: 10, map 13, 1950b: 32; 1951: 28; Pettibone, 1954: 236–238, fig. 27, d (synonymy); Ushakov, 1955: 91, fig. 2, A, B, fig. 3, A, B; Eliason, 1962a: 19 (Anaitides); Pettibone, 1963: 80–81, fig. 18, e; Imajima, 1963: 351 (Anaitides); Hartman, 1965: 59 (Anaitides).

Cephalic lobe with a large posterior incision and distinct occipital papilla in a depression; small retractile nuchal processes at the posterior margin of the cephalic lobe at the base of the 1st pair of tentacular cirri. Distal part of proboscis tuberculate (tubercles usually arranged in 6 fairly distinct longitudinal stripes); 17 marginal papillae. Proximal part of proboscis with 6 longitudinal rows of conical yellowish brown papillae on each side; 12–15 papillae in each row (not more than 8–10 papillae in 4 or 5 longitudinal rows in juvenile specimens). Dorsal tentacular cirri of 2nd segment the longest (if drawn posteriorly, they reach the 9th—11th setigerous segment). Setae absent on 2nd segment, present on 3rd segment. Formula of anterior segments: $(1 + O\frac{1}{1}) + S\frac{1}{N}$.

Dorsal cirri on anterior segments oblong-oval, slightly pointed, irregularly
134 rhomboidal on the middle segments, with truncate end, partly covering the dorsal side of the segments. Ventral cirri blunt anteriorly, pointed, with an asymmetrical pointed end, larger than the podial lobe further posteriorly.

Coloration greenish brown, with dark transverse stripes on dorsal side of segments; dorsal cirri greenish with brown spots, sometimes dark brown with a light margin; the coloration becomes slate-gray in alcohol, iridescent with colors of the rainbow.

Number of segments to 700. Often very large: length 300 mm, width including the parapodia 6 mm.

Mature females with numerous eggs in the parapodia recorded from the Far Eastern seas from April to September.

Remarks. A color variation, orientalis, in which the spots on the dorsal side are fused in the median line and form a single longitudinal dark stripe in the anterior part of the body, has been described by Zaks (1933) from the Far Eastern seas. The material examined shows that the pigmentation varies markedly, and it is not always possible to identify orientalis with certainty.

Distribution. The ZIN collection contains numerous specimens from the northern and Far Eastern seas (about 500 localities). The species usually lives in depths of to 200 m, but has been recorded in the Sea of Japan at a depth of about 1000 m; it occurs mainly on silty ground with pebbles and stones; it forms colonies with a density of 12 worms per m^2 near the coast of Southern Sakhalin.

A widely distributed Arctic-boreal species: circumpolar in the Arctic Region, extending south in the North Atlantic to Massachusetts Bay and the English Channel, and to the Sea of Japan and the coast of California in the Pacific (depth of distribution to 1500 m).

5. **Phyllodoce (Anaitides) maculata** (Linné, 1767) (Plate V, Figure 7)

Malmgren, 1865 : 97, pl. XIV, fig. 30 (Ph. teres); 1867 : 21—22, pl. II, fig. 8 (Ph. pulchella); 23, pl. III, fig. 16; 23—24, pl. II, fig. 11 (Ph. rinki); McIntosh, 1908 : 89—92, pl. XLV, fig. 2, pl. XLVIII, fig. 3, pl. LVIII, figs. 21, 24, pl. LXVIII, figs. 7—8, pl. LXXVIII, figs. 23—24; Bergström, 1914 : 145—147, fig. 45 (synonymy); Deryugin, 1915 : 332; Ditlevsen, 1917 : 59—60; Fauvel, 1923 : 152, fig. 53, a—e; Deryugin, 1928 : 239; Zaks, 1933 : 127; Zatsepin, 1948 : 111, pl. XXIX, fig. 3, b, c (Anaitides); Berkeley and Berkeley, 1948 : 46, fig. 67; Ushakov, 1948a : 27; 1950 : 170; Wesenberg-Lund, 1950b : 34—35, map 8; 1951 : 27; Ushakov, 1955a : 91, fig. 3, B; Khlebovich, 1961 : 161; Pettibone, 1963 : 78—80, fig. 18, d (synonymy); Imajima and Hartman, 1964 : 59, pl. 12, figs. a—c (Anaitides); Levenshtein, 1966 : 6.

Cephalic lobe with a shallow posterior incision and a small occipital papilla. Distal part of proboscis hexahedral, with transverse folds; 16—17 marginal papillae; proximal part of proboscis with 12 longitudinal rows of brown papillae (6—8 in a row). Tentacular cirri, if drawn posteriorly, reaching to the 6th—10th setigerous segment. Setae absent on the 2nd segment, present on the 3rd segment; formula of anterior segments: $(1 + O\frac{1}{1}) + S\frac{1}{N}$.

Dorsal cirri on anterior segments oblong-oval, asymmetrical with slightly
135 pointed end on the middle segments, slightly extending to the dorsal side. Ventral cirri broadly oval, rounded, slightly longer than the podial lobe.

Coloration yellowish green, with small, dark brown transverse stripes and spots on the dorsal side of the segments and at the base of the parapodia; dorsal cirri with weak brown dots. Number of segments 200—250? Length to 100 mm, width to 3 mm.

Ripe eggs in the body cavity of Ph. maculata were observed in the Kola Gulf from January to March, batches of eggs on coastal seaweed in April (Ushakov, 1925); in Dal'nie Zelentsy Bay (Eastern Murmansk) eggs were found from May to October (Kuznetsov and Matveeva, 1948); mature females with numerous eggs in the parapodia were recorded in May in the White Sea. Egg batches greenish. About 150,000 eggs per batch (Petrovskaya, 1950). In the littoral of the Kuril Islands, mature specimens were found in December and April (Khlebovich, 1961).

Distribution. About 200 specimens in the ZIN collection are from the Barents, White and Bering seas, the Sea of Okhotsk and Sea of Japan and from the South Kuril Islands; depth: 0—300 m, but mainly not below 50 m; in Anadyr Bay (Bering Sea) colonies are formed in the sublittoral with a density of 40 individuals per m^2, or 4.7 g/m^2 (Levenshtein, 1966). The species has been recorded from the Pacific coast of Canada (Vancouver); Hokkaido; in the North Atlantic from the west coast of Greenland, the Atlantic coast of North America to Massachusetts Bay; also Iceland, the Faeroes, coast of Norway; in the North Sea, spreading into the western Baltic, the English Channel; recently recorded from the coast of West Africa, Ivory Coast (Guy, 1964) and from the Black Sea (Vinogradov, 1949).

6. **Phyllodoce (Anaitides) mucosa** Oersted, 1843 (Plate VI, Figure 1)

Malmgren, 1867 : 27, pl. II, fig. 7; Webster and Benedict, 1887 : 710; Bergström, 1914 : 143—144, fig. 43; Fauvel, 1923 : 152—153, fig. 54, a—e; Hartman, 1948a : 19; Berkeley and Berkeley, 1948 : 46, fig. 68; Støp-Bowitz, 1948 : 16; Wesenberg-Lund, 1950a : 10, map 13, pl. I, fig. 3; Banse, 1959 : 422; Eliason, 1962a : 19; Pettibone, 1963 : 81—82, fig. 18, f, g.

Cephalic lobe as in Ph. maculata. Distal part of proboscis hexahedral, with transverse folds; proximal part with 12 longitudinal rows of papillae (8—10 in each row). If the tentacular cirri are drawn posteriorly, they reach to the 8th or 10th setigerous segment. Setae absent on the 2nd segment, present on the 3rd. Formula of anterior segments: $(1 + O\frac{1}{1}) + S\frac{1}{N}$.

Dorsal cirri oblong-oval on the anterior body segments, irregularly longer and pointed on the middle segments, 1.5 times longer than wide; ventral cirri long and pointed, almost twice as long as the podial lobe.

136 Coloration: muddy gray, with brown stripes (spots) medially and laterally (at the base of the parapodia) on all segments, so that there are 3 dark longitudinal stripes on the dorsal side; dorsal cirri light-colored, weakly

pigmented or with dark spots in the middle. Number of segments 100–200. Length 100–150 mm, width 2–3 mm.

Remarks. Differs from Ph. maculata (Linné) in its more elongate and pointed ventral cirri. It has been recorded from the White Sea (Deryugin, 1928; Sveshnikov, 1951) and from the Barents Sea (Zatsepin, 1948), but this needs confirmation; juvenile Ph. (A.) groenlandica Oerst. may have been mistaken for Ph. (A.) mucosa Oerst. in these cases.

Distribution. The ZIN collection contains specimens from the Black Sea, Kerch Strait, Odessa Bay, littoral of Rumania, depth 41–87 m, and from the Atlantic coast of France (Roscoff). It has been recorded from the east coast of America, from Labrador (Hudson Bay) to the Gulf of Mexico; coast of Iceland, Faeroes; North Sea, Oresund, English Channel; Mediterranean; Azores; coast of West Africa; also in the Pacific Ocean from Alaska to Southern California and Mexico. Depth 0–425 m.

7. **Phyllodoce (Anaitides) citrina** Malmgren, 1865 (Plate V, Figures 5, 6)

Malmgren, 1865 : 45, pl. XIII, fig. 24; Théel, 1879 : 35; Marenzeller, 1900 : 2; Moore, 1908 : 328; Bergström, 1914 : 140–141, fig. 41; Fauvel, 1923 : 150, fig. 52, k–l; Berkeley, 1924 : 287; Augener, 1928 : 705; Deryugin, 1928 : 239; Zaks, 1929 : 42; Hartman, 1948a : 19–20; Zatsepin, 1948 : 111, pl. XXIX, fig. 5, b, c; Berkeley and Berkeley, 1948 : 45, fig. 63; Wesenberg-Lund, 1960b : 32, map 8; Ushakov, 1955a : 91, fig. 3, D; Eliason, 1962a : 18.

Cephalic lobe broad, occipital papilla distinct. Distal oblong part of proboscis cylindrical, smooth or with 6 longitudinal rows of indistinct transverse folds and tubercles; 17 marginal papillae. Eight longitudinal rows of 3–6 dark papillae in proximal part of proboscis (longitudinal rows of papillae at sides of pharynx, 4 rows on each side). The tentacular cirri, if drawn posteriorly, reach to the 10th–11th setigerous segment. Setae absent on 2nd segment, present on 3rd. Formula of anterior segments: $(1 + O\frac{1}{1}) + S\frac{1}{N}$.

Dorsal cirri rounded on anterior body segments, transverse-oval on middle segments, distinctly extending to the dorsal side. Ventral cirri broad, as long as or slightly longer than the podial lobe.

Coloration greenish yellow or brown (slate gray in alcohol), with dark transverse spots on the dorsal side of the segments in the middle, so that there is a dark longitudinal stripe in the median line; dorsal cirri yellowish, lighter than dorsal side of segments. Number of segments 150–200. Length to 200 mm, width 6 mm.

Remarks. Small eyes have been reported for this species (Fauvel,
137 1923; Berkeley and Berkeley, 1948), but specimens with very large eyes, as in Ph. groenlandica Oersted, have been found.

Distribution. There are 60 specimens in our collection. The species occurs in all northern seas and in the Far Eastern seas, but more rarely than Ph. groenlandica Oerst.; depth 10–270 m. It has been recorded from the west coast of Greenland (Wesenberg-Lund, 1950b), the North Sea (Friedrich, 1938), Oresund (Eliason, 1962a) and also from the Gulf of Alaska (Hartman, 1948a) and the west coast of Canada (Berkeley and Berkeley, 1948).

8. **Phyllodoce (Anaitides) chinensis** Uschakov and Wu, 1959 (Plate VI, Figures 2–4)

Ushakov and Wu Pao-ling, 1959 : 22–23, pl. I, A–B; 1965 : 147–148.

Cephalic lobe broad, with a shallow occipital incision and an occipital papilla. Nuchal papillae at sides of cephalic lobe distinct. Proboscis very large, cylindrical (to 7 mm long); 6 lateral longitudinal rows of papillae in its proximal part on each side, close to each other, to 9 elongate papillae in each row; an additional isolated group of papillae consisting of 2 longitudinal rows on the dorsal side of the proboscis (to 5 papillae in each row). Seventeen marginal papillae at the outer margin of the proboscis. The longest tentacular cirri are the dorsal cirri on the 2nd and 3rd segment, which extend to the 11th segment. Setae absent on 2nd and 3rd segment. Only a small tubercle on 3rd segment instead of a normal neuropodium. Formula of anterior segments: $(1 + O\frac{1}{1}) + O\frac{1}{O}$.

Dorsal cirri broadly oval or bean-shaped, much wider than long. Ventral cirri slightly pointed, extending slightly beyond the podial lobe. Numerous oblong glands at the margin of the dorsal and ventral cirri.

Dorsal cirri yellowish green. A dark longitudinal stripe on the dorsal side (as in Ph. (Anaitides) groenlandica v. orientalis Zachs). Over 200 segments. Length to 160 mm, width including the parapodia, 5 mm.

Remarks. This species is characterized by the absence of a normally developed neuropodium on the 3rd segment, and O is shown instead of N for the 3rd segment in the formula. There is a mistake in the formula published in 1965: O is shown for the 2nd segment). The species resembles Ph. (A.) groenlandica and Ph. (A.) citrina in the form of the dorsal cirri but differs from them in the absence of setae on the 3rd segment and in the number of longitudinal rows of papillae in the proximal part of the proboscis. Additional rows of single papillae on the dorsal side of the proboscis have been recorded for several species, particularly for Ph. (A.) madeirensis (see below), which, however, has different dorsal cirri.

Distribution. Yellow Sea – Tsingtao, littoral and upper horizons of the sublittoral to a depth of 8 m (type deposited at the Institute of Oceanology, Republic of China, Tsingtao; cotype in the ZIN collection).

138 9. **Phyllodoce (Anaitides) madeirensis** Langerhans, 1880 (Plate VI, Figures 7, 8)

Langerhans, 1880 : 307, pl. XVII, fig. 44; Fauvel, 1919 : 361–364, fig. II (synonymy); 1923 : 150–151, fig. 23, d–h; Treadwell, 1926 : 12–13, pl. 2, figs. 19–21 (Ph. pulla); Fauvel, 1932 : 70 (synonymy); Okuda, 1937b : 269–270, fig. 10; Fauvel, 1939 : 275; (nec Berkeley and Berkeley, 1948 : 45; cf. Hartman and Reish, 1950 : 11. = Anaitides medipapillata (Moore, 1909)); Wesenberg-Lund, 1949 : 272–273; Fauvel, 1953 : 120–121, fig. 59, d–h; (nec Friedrich, 1956 : 57–58); Fauvel and Rullier, 1957 : 60–62 (synonymy); Day, 1960 : 296–297; Imajima and Hartman, 1964 : 60 (Anaitides); Rullier, 1964 : 197; 1965a : 21.

Cephalic lobe with a deep posterior incision and distinct occipital papilla. Two large, black eyes. Proboscis with 12 longitudinal rows of papillae in proximal part (6 rows on each side of the proboscis); 8–12 papillae in each row; in addition, there is sometimes a 13th row of 4–6 papillae on the dorsal side of the proboscis. Setae absent on 2nd and 3rd segment; formula: $(1 + O\frac{1}{1}) + O\frac{1}{N}$. Dorsal tentacular cirri of 2nd segment, if drawn posteriorly, reaching to the 12th segment. Dorsal cirri of anterior segments relatively small, regularly lanceolate; they are very large, long, pointed, of irregular form in the middle of the body; ventral cirri pointed, slightly longer than the podial lobe.

Dorsal side of segments of our specimens (kept in alcohol) weakly pigmented (with indistinct transverse striation), dorsal cirri of lighter color than dorsal side of segments. Specimens from the littoral of Japan (Imajima and Hartman, 1964) are light yellowish gray to brown, with dark violet reflexes; cirri, parapodia and ventral side brown. Over 300 segments (Okuda, 1937b). Length over 100 mm (a damaged specimen from Hainan was 90 mm long and about 2 mm wide).

Remarks. According to Hartman (1959 : 143), Ph. (A.) madeirensis is closely related to Anaitides erythrophyllus (Schmarda, 1861) from the West Indies and the Gulf of Mexico. Records of Ph. (A.) madeirensis from the Antarctic and Subantarctic (Ehlers, 1897, 1913; Willey, 1902; Benham, 1927) are erroneous – the specimens from these regions belong to Ph. (A.) patagonica (Kinberg, 1886), in which setae are always present on the 3rd segment, while the opposite is the case in typical P. (A.) madeirensis (Ushakov, 1962 : 138).

Distribution. The ZIN collection contains a mature female (numerous eggs in the parapodia) from Hainan Island, from a coral reef, collected in May 1958, and 4 specimens from the Gulf of Tonkin, depth 29–42 m, January 1960.

This is a widely distributed, mainly tropical species. It occurs off the coasts of France, Spain, West Africa, Madagascar, India, Indo-China, Malay Archipelago, Philippines, Japan, Australia, New Caledonia, Galapagos Islands and California.

139 10. **Phyllodoce (Anaitides) papillosa** Uschakov and Wu, 1959 (Plate VI, Figures 5, 6)

Ushakov and Wu Pao-ling, 1959 : 23–24, pl. I, D, E; Kao, 1959 : 141, pl. VI, fig. 1, a–c (Phyllodoce sp.); Ushakov and Wu Pao-ling, 1965 : 148–149, fig. 1, D, E (nec Paranaitis papillosa (Ehlers, 1887)).

Cephalic lobe slightly oblong, with an occipital incision and a small, indistinct occipital papilla; 2 large eyes, lens sometimes visible. On each side of posterior margin of the cephalic lobe there are retractile nuchal processes (difficult to see in a specimen with retracted pharynx). Proboscis distinctly divided into a distal and a proximal part. There are 12 longitudinal rows of pigmented papillae in the proximal part (6 rows on each side). Distal part of proboscis covered on all sides with large teat-shaped papillae, so that it appears shaggy. The longest tentacular cirri are the dorsal cirri on the 2nd and 3rd segment, which reach the 9th segment. Setae absent on 2nd and 3rd segment. Formula of anterior segments: $(1 + O\frac{1}{1}) + O\frac{1}{N}$.

Dorsal cirri on body segments of irregular, slightly oblong form (longer than wide), situated on high cirrophores. Ventral cirri pointed, slightly projecting beyond the podial lobe. Secondary annulation distinct on the dorsal side.

Coloration of specimens preserved in alcohol uniformly light to dark beige, the 3rd–5th segment the darkest. Dorsal cirri sometimes slightly pigmented in middle of body. In mature females, ventral side and parapodial appendages reddish due to the eggs shining through. To 270 segments. Length 120 mm, width including the parapodia 2.5 mm.

A mature female with eggs was recorded in June; its dorsal cirri are broader than in other specimens.

Remarks. Imajima (1967) described the new species Ph. japonica Imajima, 1967 from the western littoral of Japan (Noto Peninsula), which differs from the species described here only in the absence of nuchal processes on the posterior margin of the cephalic lobe (but these organs are retractile and possibly were retracted in Imajima's specimen, and hence overlooked), in the darker coloration of the anterior segments and in the spherical distal papillae on the proboscis of Ph. japonica (pointed in Ph.(A.) papillosa); also, the papillae in the proximal part of the proboscis are arranged in 10 rows, not in 12 as in Ph.(A.) papillosa. The last character is the most important, but Imajima unfortunately had a specimen in which the proboscis was retracted, and the number of rows of papillae could be counted only in a dissection of the proboscis, which does not give an exact picture. If the two species are not identical, they are certainly closely related. Hartman (1961 : 63) recorded from the coast of California a Phyllodoce sp., which in his opinion is closely related to Ph. papillosa Uschakov and Wu, and differs from it only in its smaller size. The presence of large lanceolate papillae at the distal end of the proboscis in Ph. papillosa resembles the case in Ph. macropapillosa Saint-Joseph, 1895, but Ph. papillosa differs in the absence of setae on the 2nd and 3rd segment.

Type deposited at the Institute of Oceanology at Tsingtao.

140 Distribution. The ZIN collection contains 19 specimens from the Yellow Sea – Tsingtao and Cheifoo bays, littoral and upper sublittoral horizons; a similar specimen was found near the coast of Hainan. The species is apparently endemic in subtropical waters of the Northwest Pacific.

6. Genus **PARANAITIS** Southern, 1914

(= Anaitis Malmgren, 1865 (praeoccup. Duponchel, 1829, pro Lepidoptera))

Cephalic lobe broadly oval, its posterior margin rounded or conical; occipital ligula covered by the nuchal papilla at the end. Four cephalic tentacles. One pair of eyes, often with a distinct lens, or without a lens. Proboscis with lateral longitudinal rows of large papillae. Border between 1st and 2nd segment indistinct; these segments are distinctly larger than the following and form a "collar" which surrounds the cephalic lobe laterally. Four pairs of cylindrical or slightly flattened tentacular cirri. Formula of anterior segments: $(1 + O\frac{1}{1}) + S\frac{1}{N}$. Parapodia uniramous. Dorsal cirri broad, bean-shaped, very large, partly covering the dorsal side (superficially resembling the dorsal scales of Polynoidae). All setae segmented.

Type species: Anaitis wahlbergi Malmgren, 1865.

The genus contains about 12 species. Two species in Soviet waters: in the Arctic seas P. wahlbergi (Malmgren) and in the Far Eastern seas P. polynoides (Moore); east of Honshu P. caecum n. sp., collected by the "Vityaz").

Key to species of the genus Paranaitis Southern

1 (4). Eyes present.
2 (3). Cephalic lobe with rounded posterior margin, without distinct occipital ligula or nuchal papilla. Coloration greenish brown, dorsal cirri yellowish olive . . . . 1. **P. wahlbergi** (Malmgren)
3 (2). Cephalic lobe at posterior end with an elongate occipital ligula with a nuchal papilla. Coloration light beige, with a median reddish brown stripe on the dorsum; dorsal cirri also light beige, but with a median dark spot, the spots becoming fused into two lateral longitudinal stripes along the entire body . . . . 2. **P. polynoides** (Moore)
4 (1). Eyes absent. . . . . 3. **P. caecum** Uschakov

1. **Paranaitis wahlbergi** (Malmgren, 1865) (Plate VII, Figures 8, 9)

Malmgren, 1865 : 94, pl. XIV, fig. 31 (Anaitis); Théel, 1879 : 35 (Anaitis); Wiren, 1883 : 401 (Anaitis); Marenzeller, 1892 : 405–407 (Anaitis); Fauvel, 1911 : 26 (Anaitis); Bergström, 1914 : 155–156, textfig. 51 (Anaitis); Augener, 1928 : 705–706 (Anaitis); Annenkova, 1932a : 168 (Anaitis); Gorbunoc, 1946 : 38 (Anaitis); Zatsepin, 1948 : 112 (Anaitis); Wesenberg-Lund, 1950a : 10, map 13; 1951 : 25; 1953 : 30 (Anaitis); Hartman, 1965a : 62.

141 Cephalic lobe with broadly rounded posterior margin, without distinct occipital ligula; nuchal papilla indistinct. Two large eyes. Proboscis thin, very long, smooth in its small proximal part, strongly pigmented dorsally; other part of proboscis with 2 longitudinal rows of lateral papillae. First and 2nd segment fused dorsally, nearly twice as wide as the cephalic lobe. Tentacular cirri reaching about the 5th setigerous segment. Secondary annulation distinct on dorsal side of body segments. Dorsal cirri on anterior segments smaller than on following segments. They are broadly oval in the middle of the body, bean-shaped, large, covering a large part of the dorsum; base of dorsal cirri low and broad. Ventral cirri large, leaf-shaped, with an incision at the ventral margin. Podial lobe bifid, upper lip larger than the lower; both lips rounded. Aciculum light yellow, very long and elastic; it is sometimes curved and pressed against the dorsal margin of the podial lobe. Setae long, thin, numerous (over 100 setae in a bundle). Articular denticles of rostrum of setae with spines of varying size; distal part long.

Coloration of specimens preserved in alcohol greenish brown with a slight iridescence; ventral side slightly lighter than the dorsal; dorsal cirri yellowish olive. Very large worms; number of segments over 200; length

125 mm, width to 15 mm including the parapodia and setae (12 mm without the setae); body markedly flattened.

Mature specimens recorded in September; eggs entering the cavity of the podial lobe.

Remarks. Some authors (Southern, 1914; Ditlevsen, 1917) consider P. wahlbergi (Malmgren) and P. kosteriensis (Malmgren) as the same species, but comparison of P. wahlbergi from the Arctic with P. kosteriensis from the Kattegat (coll. Eliason) proves that they are distinct. In P. wahlbergi, the posterior margin of the cephalic lobe is rounded, but it has a ligula in P. kosteriensis; P. kosteriensis is also smaller than P. wahlbergi. The coloration is also different: P. wahlbergi is greenish, P. kosteriensis reddish brown. P. kosteriensis has been recorded from the West coast of Sweden, the littoral of Denmark, Scotland and Ireland and also from Labrador (Pettibone, 1956, 1963).

Distribution. The ZIN collection contains about 60 specimens from the Barents Sea, Franz Josef Land, Novaya Zemlya, the Kara Sea and Novosibirsk Islands; general depth 30–460 m. It has been recorded from Spitsbergen, Greenland, Jan Mayen Island, Iceland and the North Sea to the Kattegat; at a depth of 1200 m in the Norway Sea (Hansen, 1882 : 22). Mainly an Arctic species.

2. **Paranaitis polynoides** (Moore, 1906) (Plate VII, Figures 1–4)

Moore, 1909a : 339–342, pl. XVI, figs. 19–21 (Anaitis); Berkeley, 1924 : 287 (Anaitis); Zaks, 1933 : 127 (Anaitis); Annenkova, 1937 : 156; 1938 : 141–142 (Phyllodoce (Anaitis)); Berkeley and Berkeley, 1948 : 44, fig. 62 (Phyllodoce (Paranaitis)); Ushakov, 1955a : 94, figs. 2, C, D and 3, E, F.

142 Cephalic lobe with a distinct occipital ligula situated in a depression on the 1st segment; a distinct nuchal papilla at the posterior end of the ligula; length of cephalic lobe without occipital ligula about half its width. Two large eyes; lens sometimes distinct. Proboscis trihedral, mouth surrounded by numerous marginal papillae, the two largest conical papillae directed into the opening; distal part of pharynx with numerous distinct transverse folds arranged in 6 longitudinal stripes, the lateral stripes most strongly convex; proximal part of proboscis with lateral longitudinal rows of a few rounded papillae. First segment fused dorsally with the 2nd or indistinctly separated from it by a groove. Tentacular cirri cylindrical, slightly flattened, situated on high cirrophores; upper tentacular cirri on 2nd segment and all tentacular cirri on 3rd segment distinctly longer than the others; if drawn posteriorly, they reach the 6th–8th setigerous segment; dorsal cirri on anterior segments rounded, transverse-oval on the other segments, very large, slightly extending onto the dorsal side and covering a large part of the dorsum; ventral cirri oblong-oval, about as large as the podial lobe. Podial lobe bifid, the upper lip slightly larger than the lower. Aciculum light yellow. Setae numerous, about 50 in a bundle. Articular denticles of rostrum of setae with 2 transverse rows of small spines; distal part long, with small denticles on the inner margin. Anal cirri long, 3 times as long as wide.

Coloration very characteristic: on the light beige background of the dorsal side is a distinct reddish brown longitudinal median stripe with a blue sheen; each dorsal cirrus has a dark spot in the center; the spots are fused into two longitudinal lateral stripes; ventral side without coloration; tentacular cirri of a weak reddish color. To 85 setigerous segments. Length to 45 mm, maximum width including the parapodia and setae 4 mm.

Remarks. P. polynoides resembles P. speciosa (Webster, 1880), recorded from the Atlantic coast of North America – Chesapeake Bay (Pettibone, 1963), but P. speciosa has no nuchal papilla, and there are broad, dark transverse stripes on the 9th and 10th segment which are absent in P. polynoides.

Distribution. Sea of Japan (Peter the Great Bay, Tatar Strait, littoral of Southern Sakhalin), near the southern Kuril Islands and Gulf of Tonkin; depth 8–286 m (34 specimens). A North Pacific species, recorded from the southeastern littoral of Kamchatka, west coast of Canada and from the coast of California, Monterey Bay and Los Angeles.

3. **Paranaitis caecum** Uschakov, n.sp. (Plate VII, Figures 5–7)

Cephalic lobe with a distinct occipital ligula; nuchal papilla large. Eyes absent. Proboscis oblong (not examined). First segment of the larger specimen separated from the 2nd segment by a thin line, the border between the 143 segments not visible in the smaller specimen. First segment much broader than the cephalic lobe. Tentacular cirri on 3rd segment reaching the 8th or 9th segment. Dorsal cirri broad, slightly asymmetrical, bean-shaped, covering a large part of the dorsal surface; dorsal cirri with large gland cells, mainly at the outer margin. Ventral cirri slightly shorter than the podial lobe. Upper lip of podial lobe larger than the lower lip. Aciculum of light color, large. Setae numerous, with long distal part; rostrum with a large articular denticle, distal part finely serrate.

Body uniformly light; dorsal cirri half light, half yellowish green, forming two longitudinal dark stripes in the median line. Number of segments of the larger specimen 62. Length to 20 mm, width including the parapodia but without the setae 2 mm; length of distal part of setae 0.1–0.5 mm.

We have 2 specimens, the larger of which has been designated as the type.

The type is deposited at ZIN, No. 1/16140 ("Vityaz," station 3580).

Remarks. This species resembles P. polynoides (Moore) in some characters, but differs from it in the absence of eyes, the longer tentacular cirri and the slightly different form of the dorsal cirri.

Distribution. Northwest Pacific – east of Honshu: 38°38' N and 141°53' E, depth 239 m ("Vityaz," station 3580, May 1957, type) and 38°36 N and 142°12' E, depth 598 m ("Vityaz," station 3579, one specimen).

7. Genus **CHAETOPARIA** Malmgren, 1867

Cephalic lobe indistinctly separated from 1st segment. Four frontal tentacles and a median elongate papilla at the posterior margin of the cephalic lobe. Proboscis diffusely covered with small papillae. First and 2nd segments fused. Third segment indistinctly separated. Four pairs of tentacular cirri. Formula of anterior segments: $(1 + C\frac{1}{1}) + C\frac{1}{O} + C\frac{N}{n} + S\frac{N}{N}$. Simple, golden, hook-shaped setae on the 2nd–4th segment, segmented setae with long distal part on the following segments.

The genus contains only one species, Chaetoparia nilssoni Malmgren, 1867.

Our diagnosis of the genus differs slightly from that of Bergström (1914: 88–90); the reasons are given in the description of the species. The description is based on a specimen collected near the Kristineberg Biological Station (Sweden) at a depth of 35 m, by Eliason (Museum of Natural History, Göteborg); the specimen is deposited at ZIN, No. 1/15184.

1. **Chaetoparia nilssoni** Malmgren, 1867 (Plate XIV, Figures 5–10)

Malmgren, 1867: 29, pl. II, fig. 5, a–d; Bergström, 1914: 169–172, pl. II, fig. 2; pl. III, fig. 3, textfig. 60.

Cephalic lobe with a pair of sunken, indistinct eyes. Proboscis only partly
144 everted, covered with small granules in its lower part. First and 2nd segments forming a broad "collar" at the sides of the cephalic lobe, as in Paranaitis; they bear 3 pairs of elongate tentacular cirri. Before and slightly below the ventral cirri of the 2nd segment is a small transverse fold, from which project small, straight, golden, needlelike setae (5–6 on each side). Distinct lateral tubercles (cushions) on the ventral side of the 3rd segment, from the anterior margin of which project large, simple, slightly curved, golden setae with a lateral lobe (Plate XIV, Figure 10) which form a dense transverse row. Only one pair of tentacular cirri on the 3rd segment; a neuropodium is absent (!). The longest tentacular cirri are the 2nd dorsal and the 3rd; they extend to the 7th segment. Fourth segment: dorsal cirrus, resembling in form and size the cirri on the rest of the body segments (Bergström considers this dorsal cirrus as the ventral cirrus of the 3rd segment), and a very small ventral cirrus (apparently overlooked by Bergström); a podial lobe is absent on the 4th segment between the dorsal cirrus and the ventral cirrus, but at its anterior margin, at the border with the 3rd segment, there are several simple, needlelike setae which project from the ventral side of the segment: 3 or 4 larger setae more laterally, and 4 very small setae in the median part (Bergström places these setae on the 3rd segment). All the following segments are of normal structure. Dorsal cirri oval spoon-shaped, situated on high cirrophores with an elongate process which envelops the dorsal side of the cirrus, more than half as long as the cirrus; on the outer margin of this process is a stripe of ciliary epithelium. Ventral cirri markedly larger than the podial lobe. Podial lobe slightly bifid, with one aciculum and a bundle of about 12 complex setae, their distal part elongate and flexible. Anal cirri very long, about 10 times as long as wide, with pointed end (about 0.5 mm long).

Coloration of body of the specimen preserved in alcohol light beige; a darker transverse stripe on the dorsal side of each segment from parapodium to parapodium; dorsal cirri slightly darker than body, small dark dots on some of them. About 100 segments, last segments underdeveloped. Length 30 mm, width including the parapodia with setae 2 mm.

Remarks. This species differs from all other species of benthic Phyllodocidae in the presence of hook-shaped golden setae on the 2nd–4th anterior segment. The morphological functional causes of the appearance of these large setae on the anterior segments are not clear (it would be understandable if these worms were to inhabit tubes, but there are no records of this). Even larger hook-shaped setae on the 2 or 3 anterior trunk segments have been observed only in the pelagic Lopadorhynchus (these setae may serve for holding the prey). The presence of simple hook-shaped setae on the last segments of Chaetoparia and Lopadorhynchus, and the fusion of the cephalic lobe with the 1st segment show that these two genera are closely related, despite the fact that Chaetoparia contains benthic species and Lopadorhynchus is a typical pelagic, highly specialized 145 genus (p. 174). There are here possibly indications of relationship and common origin; it is more difficult to assume that this is a case of parallel development, as these forms have a quite different ecology.

Distribution. The Kattegat.

8. Genus **EULALIA** Savigny, 1817

(incl. Hypoeulalia Bergström, 1914)

Cephalic lobe slightly oblong, rounded or slightly pointed anteriorly. Five cephalic tentacles: 4 at the anterior end and one on the dorsal side of the cephalic lobe near the posterior margin. One pair of usually large eyes, sometimes also with small eye spots, or eyes absent. Three anterior segments distinctly separated from each other and from the cephalic lobe. Four pairs of spindle-shaped tentacular cirri. Setae present or absent on the 2nd segment, always present on the 3rd segment. Formula: $1 + S\frac{1}{1} + S\frac{1}{N}$ or $1 + O\frac{1}{1} + S\frac{1}{N}$. Proboscis with papillae, which are diffusely arranged or forming 6 longitudinal stripes in the distal part. Parapodia uniramous. All setae segmented, but simple, long hairlike setae sometimes appear in epitokous mature forms.

Type species: Nereis viridis Linné, 1767 (O.F. Müller, 1776).

There are about 40 species in this genus, but the systematic position of many of them is not clear. Five species in the Polar Basin and Northwest Pacific. The new species Eulalia sphaerocephala R. Ya. Levenshtein (1961) has been transferred to the genus Austrophyllum (p. 155).

Fauvel (1923) and other authors include Eumida Malmgren and Pterocirrus Claparède as subgenera in the genus Eulalia; however, they are considered here as valid genera, which differ from Eulalia sensu stricto in the reduction of the 1st segment.

Bergström (1914) proposed the new genus Hypoeulalia for the species Eulalia bilineata (Johnston, 1840) and E. subulifera Ehlers, 1897, because the 1st segment is fused with the cephalic lobe in these species. However, careful examination of E. bilineata usually shows the border between the cephalic lobe and the 1st segment, and this species should therefore be placed in the genus Eulalia sensu stricto. As regards Eulalia subulifera, recorded from the Antarctic, there is apparently confusion between two different species. Ehlers (1897) described E. subulifera and stated that all 3 anterior segments are separated from each other and from the cephalic lobe in juvenile specimens, while the 1st and 2nd segments are fused in adults. Such a modification due to age seems unlikely and requires confirmation. In our specimens of Eulalia subulifera from the Antarctic (Ushakov, 1962) which are only about 0.5 cm long, the two first segments are fused dorsally and they should therefore be placed in the genus Eumida Malmgren. Gravier (1907) described as Eul. subulifera specimens in which all three anterior segments were distinctly separated, as in typical species of the genus Eulalia sensu stricto.

146 Key to species of the genus Eulalia Savigny

1 (6). Proboscis with diffusely arranged papillae.
2 (3). Dorsal cirri oblong-oval, with blunt, rounded end . . . . 2. **E. bilineata** Johnston
3 (2). Dorsal cirri elongate, with fine, pointed end.
4 (5). Eyes present. Podial lobe with short, rounded upper and lower lips of equal size . . . . 1. **E. viridis** (L.)
5 (4). Eyes absent. Podial lobe with elongate pointed upper lip and short rounded lower lip . . . . 3. **E. sigeformis** Annenkova
6 (1). Proboscis with 6 longitudinal rows of large papillae in the distal part.
7 (8). Tentacular cirri long (reaching to the 12th segment). . . . . 4. **E. austrophylloformis** Uschakov
8 (7). Tentacular cirri short (reaching to the 7th segment) . . . . 5. **E. gravieri** Uschakov

1. **Eulalia viridis** (Linné, 1767) (Plate VIII, Figures 1–4)

Malmgren, 1865: 98, pl. XV, fig. 39; McIntosh, 1908: 55–60, pl. XLIV, fig. 1, pl. XLIII, fig. 3, pl. XLVII, figs. 10–11, pl. LXXVIII, figs. 2–2a (synonymy); Izuka, 1912: 205–206, pl. XXI, fig. 6; Ditlevsen, 1914: 686; Bergström, 1914: 123–125, fig. 32; Deryugin, 1915: 322; Fauvel, 1923: 160, fig. 57, a–h; Augener, 1928: 706; Deryugin, 1928: 239; Annenkova, 1934: 322; Fauvel, 1936: 58; 1937: 157; 1938: 142; Gorbunov, 1946: 38; Ushakov, 1948a: 27; Zatsepin, 1948: 112, pl. XXIX, fig. 8, b, c, d; Hartman, 1948a: 20, fig. 5; Berkeley and Berkeley, 1948: 48–49; Vinogradov, 1949: 31–32; Ushakov, 1950: 168; Wesenberg-Lund, 1950a: 10, map 14; Ushakov, 1955a: 98, fig. 5, D–F; Khlebovich, 1961: 162; Pettibone, 1963: 85–86, fig. 19 (synonymy); Ushakov and Wu Pao-ling, 1965: 152–153; Imajima and Hartman, 1964: 63; Levenshtein, 1966: 8; Buzhinskaya, 1967: 80.

Cephalic lobe slightly elongate. Two large, black eyes (sometimes two additional small pigment spots at the sides). Single cephalic tentacle longer than paired tentacles; it is situated between the eyespots or slightly before the level of the eyes. Proboscis diffusely covered with numerous small, slightly granulate papillae (papillae sometimes absent in basal part of proboscis); 14–17, sometimes more, large papillae at the margin. Tentacular cirri cylindrical, threadlike, tapering to a point; only the shortest ventral cirri of the 2nd segment may be slightly flattened (especially in mature females); dorsal tentacular cirri of 2nd and 3rd segments reaching, if drawn posteriorly, to the 10th–12th setose segment. Setae usually absent on 2nd segment.

Dorsal cirri of body segments narrow-lanceolate with pointed end, ventral cirri small, normally not extending beyond the podial lobe, oval, obtuse or slightly pointed. Podial lobe with short, rounded upper and lower lips, of equal size. Shaft of setae widened at the end, with large spines at the arti-
147 culation; distal part finely denticulate. Anal cirri large, pointed, about 4 times longer than wide.

Coloration of live specimen: grass green in females, lighter, yellowish, in males; olive or dark brown in alcohol, sometimes with small dark spots and transverse stripes at the posterior margin on dorsal side of segment. Two color variants are distinguished: aurea Gravier and ornata Saint-Joseph (see Fauvel, 1923). Specimens from the Yellow Sea and Hainan Island turned dark violet in alcohol. Segments to 150 or 200. Length to 150 mm, width 2 or 3 mm.

Mature specimens were found in the Murmansk region from March to July (Ushakov, 1925; Petrovskaya, 1960), in the Sea of Japan and near the Kuril Islands from July to August (Khlebovich, 1961; Buzhinskaya, 1967), in the Yellow Sea in June and July (Ushakov and Wu Pao-ling, 1965), at the Atlantic coast of North America in July (Pettibone, 1963). Slimy batches of eggs are deposited on seaweed and pebbly ground; the eggs are usually greenish.

Remarks. Bergström (1914 : 124) doubted the data of McIntosh, Claparède and Ehlers and, after examination of his specimens, concluded that E. viridis always has setae on the 2nd segment. Fauvel, following Bergström, also stated in the formula of the anterior segments of E. viridis that setae are present on the 2nd segment. This is not correct: most of the numerous specimens examined of E. viridis from the northern and Far Eastern seas had no setae on the 2nd segment; this was also the case in specimens from Roscoff (4 specimens) and from the coast of Sweden (6). Ten specimens (sent by Pettibone) from Alaska and Woods Hole also had no setae on the 2nd segment. Because of the above statement by Bergström that E. viridis always has setae on the 2nd segment, Imajima and Hartman (1964) recently established a subspecies japonica for specimens of E. viridis from Japan, which had no setae on the 2nd segment. However, the establishment of a subspecies for E. viridis from the Pacific requires further study. The presence or absence of setae on the 2nd segment does not justify establishing a subspecies (this is possibly connected with age – see remarks on the genus Eteone, p. 164).

Distribution. The ZIN collection contains over 400 specimens from the Barents and White seas, the Novosibirskie Islands, Bering Sea, Kamchatka, Kuril Islands, Sea of Okhotsk, Sea of Japan, Yellow Sea and South China Sea; they were found mainly in the tidal zone (littoral baths) and in the sublittoral region among seaweed, Balanus molluscs, ascidians and under rocks and pebbles; there are isolated records from depths greater than 50 m (to 240 m); the species often occurs in large numbers, forming large colonies.

According to the literature, E. viridis has an almost worldwide distribution, but prefers boreal and subtropical waters.

148 2. **Eulalia bilineata** (Johnston, 1840) (Plate VIII, Figures 5–8)

Malmgren, 1865 : 99, pl. XIII, fig. 26, pl. XIV, fig. 29 (E. problema); McIntosh, 1908 : 50–53, pl. XLIII, fig. 5, pl. L, fig. 4, pl. XLVII, figs. 6–7, pl. LXXVII, figs. 23–24; Bergström, 1914 : 165–166, fig. 57 (Hypoeulalia); Ditlevsen, 1917 : 54, pl. IV (E. tjalfiensis); Fauvel, 1923 : 162–163, fig. 58, a–e; Augener, 1928 : 707–708; Deryugin, 1928 : 239; Annenkova, 1938 : 143; Gorbunov, 1946 : 38; Zatsepin, 1948 : 112, pl. XXIX, fig. 9, b–d (Hypoeulalia); Ushakov, 1948 : 27; Berkeley and Berkeley, 1948 : 48, fig. 71; Ushakov, 1950 : 169; Wesenberg-Lund, 1950a : 10–11, map 14, pl. 1, fig. 5; Ushakov, 1955a : 98, fig. 5, A–C; Khlebovich, 1961 : 162; Pettibone, 1963 : 86–88, fig. 20 (synonymy); Ushakov and Wu Pao-ling, 1965 : 152; Imajima, 1967 : 441; Day, 1967 : 154, figs. 5, 4, g–j.

Cephalic lobe oblong, its anterior end sometimes with a slight constriction between the paired tentacles; 2 small eyes near the posterior margin of the lobe. Cephalic tentacles elongate, medium tentacle longer than the paired tentacles, situated slightly anterior to the eyes. Proboscis with large, soft papillae. First segment partly fused dorsally with the cephalic lobe (often separated from it only by an indistinct groove). All tentacular cirri spindle-shaped, pointed at the distal end; dorsal tentacular cirri of 2nd and 3rd segments (if drawn posteriorly) reaching to the 6th–8th setose segment. Setae present on 2nd and 3rd segments.

Dorsal cirri of body segments thick, oblong-oval, with rounded end; ventral cirri of the same form, but much smaller. Podial lobe with short, upper and lower rounded lips of about the same size. Shaft of setae with spines at the end; distal part relatively short, finely denticulate. Anal cirri oblong-oval, with rounded distal end; anal cirri about twice as long as wide.

Coloration light beige or yellowish brown, of varying intensity, usually with small dark spots at the base of each parapodium, forming two dark longitudinal stripes (the spots fade in alcohol); dorsal cirri sometimes dark brown. Number of segments 100–150. Body long and thin, 30–50 mm long, 2 or 3 mm wide.

Mature specimens have been recorded from the Barents Sea in June, in the Yellow Sea at the end of May, and near the coast of Britain (McIntosh, 1908) from May to July.

Remarks. Day (1967) illustrated the cephalic end of E. bilineata with the 1st and 2nd segments fused, but all segments are distinctly separated in our specimens. E. problema Malmgren, 1865, from the west coast of Greenland, and E. tjalfiensis Ditlevsen, 1917, from Davis Strait, have accessory hairlike setae, and are probably epitokous forms of E. bilineata (Johnston). Wesenberg-Lund (1950a : 11) noted 3 anal cirri in a specimen from the Jan Mayen region, but excreta were certainly wrongly considered as the 3rd anal cirrus.

Distribution. Seas of the USSR: southwestern part of the Barents Sea (depth to 290 m), in coastal waters of Murmansk (Dal'nie Zelentsy), near
149 Spitsbergen, White Sea, north of the Novosibirskie Islands (depth 49–91 m), northern and northwestern part of the Sea of Okhotsk (depth 27–60 m), near the southern Kuril Islands (depth 0–83 m), in Aniva Bay (depth 23–30 m, and in the littoral zone in Busse Bay), as well as in the Sea of Japan; it prefers sandy ground, often settles in empty tubes of other polychaetes; our collection contains over 100 specimens. According to the literature, it occurs in the Atlantic Ocean from Davis Strait to South Carolina, on the coasts of Europe and west coast of Africa, in the Mediterranean, in the Pacific Ocean, in the littoral zone of the Yellow Sea, on the coast of Vancouver Island and Southern California; at depths from 0 to 2350 m.

3. **Eulalia sigeformis** Annenkova, 1937 (Plate VIII, Figures 9–12)

Annenkova, 1937 : 157–158, fig. 7; Ushakov, 1950 : 168; 1955a : 98, fig. 5, G, H; Levenshtein, 1966 : 8.

Cephalic lobe triangular, with markedly widened posterior margin; it is wider than long. Eyes absent. Cephalic tentacles elongate, pointed; median single tentacle slightly longer than the paired tentacles, situated in the middle of the cephalic lobe. Proboscis densely and diffusely covered with slightly oblong papillae with a smooth surface and inner reticulation. Sixteen pharyngeal papillae at margin of proboscis. First segment partly covered by overhanging posterior margin of cephalic lobe. Setae present on 2nd and 3rd segments; the border between the segments is not always distinct. Tentacular cirri cylindrical, tapering to a long point; if drawn posteriorly, the tentacular cirri of the 2nd and 3rd segments reach to the 10th–13th segment.

Dorsal cirri of body segments elongate, lanceolate, with pointed end; ventral cirri of similar form, but smaller. Podial lobe with long, pointed upper lip and short, rounded lower lip. Shaft of setae with slightly widened end with spines; distal part long, slender, with indistinct serration at the margin.

Coloration of body and cirri light brownish olive in alcohol; distinct dark spots at the end of the dorsal cirri in some specimens. To 80 segments. Length to 35 mm, width including the parapodia to 5 mm.

Type deposited at ZIN AN SSSR, No. 1/20400.

The description has been supplemented with material from the Sea of Okhotsk and the Aleutian Trench.

Remarks. The dorsal cirri on the parapodia of Eu. sigeformis Annenkova partly resemble those of Pterocirrus macroceros Grube (p. 152), but it differs from P. macroceros in the absence of eyes and the spindlelike form of the tentacular cirri.

Distribution. The ZIN collection contains 12 specimens: Sea of Japan, Peter the Great Bay (depth 480–936 m), Sea of Okhotsk – near Cape Terpeniya (Sakhalin) (depth 443–645 m), and the Aleutian Trench (depth 1685–7185 m); also recorded from the Bering Sea, Olyutorski Gulf, depth 510 m (Levenshtein, 1966).

150 4. **Eulalia austrophylloformis** Uschakov, n. sp. (Plate IX, Figures 1–5)

Cephalic lobe rounded. Eyes absent, but there is a slight darkening of the integument in the form of two very small spots in the posterior part of the cephalic lobe. Single cephalic tentacle very large (longer than the cephalic lobe), situated almost at the posterior margin of the cephalic lobe; frontal tentacles also very large, as long as the width of the cephalic lobe, the second (lower) pair of tentacles (not shown in the figure) situated on the ventral side of the cephalic lobe. Proboscis retracted in our specimen, but dissection showed that the papillae form 6 distinct longitudinal rows in the distal part, as in the genus Austrophyllum; the papillae are large, oblong, with distinct rounded formations at the margin. Tentacular cirri spindle-shaped, long; dorsal cirri of 3rd segment reaching to the 12th segment. Setae present on 2nd segment. All body segments with secondary intersegmental annulation. Dorsal cirri of body segments situated on large and high cirrophores; cirri oblong-oval, light brown. Podial lobe small, with two rounded lips of about the same size. Ventral cirrus longer than podial lobe. Anal cirri very long and pointed, more than 6 times longer than wide. Rostrum of shaft of seta with small spines; distal part serrate.

Coloration of specimen in alcohol light beige, except for the dorsal and anal cirri, which are brownish. About 95 segments. Length about 15 mm, width including the parapodia 1.5 mm; width of head less than 0.5 mm.

Type deposited at ZIN AN SSSR, No. 1/16146.

Remarks. This species closely resembles Austrophyllum sphaerocephala (Levenshtein) in the structure of the proboscis, the position of the cephalic tentacles and the presence of large cirrophores on which the dorsal cirri are situated, but it cannot be placed in the genus Austrophyllum as it has no accessory notopodial acicula. In material from the Antarctic, Averintsev (1972) found two new species of Eulalia, E. semenovi Aver. and E. sotniki Aver., in which the proboscis also bears six rows of papillae, which is characteristic for the genus Austrophyllum. These species should perhaps be considered as a subgenus of Eulalia, perhaps even a separate genus. The species described is closely related to E. sotniki Aver. from the Southern Orkney Islands, but differs from it in the form of the papillae on the distal part of the proboscis.

Distribution. East of Honshu, 39°44' N and 142°18' E, depth 366–423 m; ground – large aleurite, mixed with silt and pumice ("Vityaz," station 3569, 27 April 1957, one specimen).

5. **Eulalia gravieri** Uschakov, n. sp. (Plate IX, Figures 6–10)

Cephalic lobe semicircular. Eyes absent. Single cephalic tentacle small and indistinct, situated at the posterior margin of the cephalic lobe. Frontal
151 tentacles short. Distal part of proboscis with 6 longitudinal rows of large, oblong papillae with light, rounded formations at the margin (as in E. austrophylloformis); proximal part of proboscis densely covered with even larger, rounded, transparent papillae. All tentacular cirri spindle-shaped, short and pointed; tentacular cirri of 3rd segment barely reaching to the 7th segment; ventral cirri of 2nd segment slightly widened at the base. Setae present on 2nd segment in both specimens. Dorsal cirri of body segments oblong-oval, more than twice as long as wide, semitransparent, markedly reticulate, not situated on a cirrophore. Podial lobe short, with two lips, an upper and a lower, both of about the same size. Ventral cirrus oblong-oval and slightly larger than the podial lobe. Anal cirri about 6 times longer than wide, their distal end blunt. Setae with long, serrate distal part, rostrum of shaft with small spines; each bundle with about 10 setae. A single aciculum in all parapodia.

Coloration of specimens in alcohol light beige. To 165 segments. Length to 30 mm, width including the parapodia 1 or 1.5 mm.

The ZIN collection contains 2 specimens. The species has been named after Gravier, a specialist on Polychaeta who first described a similar proboscis in Austrophyllum charcoti (Gravier, 1911).

Type deposited at ZIN AN SSSR, No. 1/16271.

Remarks. This species is closely related to E. semenovi Averinev, from the Southern Orkney Islands (Averintsev, 1971), but differs from it in the structure of the proximal part of the proboscis: the papillae on this part are very large (they are small and numerous in E. semenovi).

Distribution. East of Honshu, 38°53' N and 142°53' E; depth 1641 m; ground – large aleurite ("Vityaz," station 3578, 11 October 1957, type); southern end of Kamchatka, 51°06' N and 158°56' E; depth 3107–3265 m ("Vityaz," station 3271, 10 May 1955, one specimen).

9. Genus **STEGGOA** Bergström, 1914

(incl. Notalia Bergström, 1914)

Cephalic lobe with 5 cephalic tentacles. One pair of large eyes. First 3 segments are fully developed and separated. Four pairs of tentacular cirri; cirri on ventral side of 2nd segment shorter than the others and markedly flattened; other tentacular cirri spindle-shaped. Setae present or absent on the 2nd and 3rd segments. Formula of anterior segments: $1 + S\frac{1}{1} + S\frac{1}{N}$, $1 + O\frac{1}{1} + S\frac{1}{N}$ or $1 + O\frac{1}{1} + O\frac{1}{N}$. Proboscis diffusely covered with numerous papillae. Parapodia uniramous. Setae segmented.

Type species: Eulalia magalhaensis Kinberg, 1866.

The type species was described from subantarctic waters, its distribution in the Antarctic is circumpolar (Ushakov, 1962). Fauvel (1919) studied this 152 species in detail and considered Eulalia tenax Grube and Pterocirrus ceylonicus Michaelson, described from the tropics, as its synonyms. It is difficult to agree with this, as setae are absent on the 2nd segment of E. magalhaensis Kinberg, and it differs distinctly from the above two species in this character.

The genus Steggoa contains about 12 species. Only one species, S. pacifica Imajima, 1964, has been recorded from the Northwest Pacific.

1. **Steggoa pacifica** Imajima, 1964 (Plate XII, Figures 12–18)

Imajima, 1964: 23–240, figs. 8–14.

Cephalic lobe triangular. Eyes absent. Single cephalic tentacle situated in posterior half of cephalic lobe. Proboscis with a ring of 13 conical papillae at the distal end; proboscis densely covered with papillae of two types: spherical papillae in distal part of proboscis, elongate, teat-shaped papillae in the basal part. First peristomal segment of cephalic lobe distinctly separated from 2nd segment and slightly longer than it. Tentacular cirri of 1st segment about as long as the cephalic lobe. Second segment with setae; ventral cirrus short and asymmetrical. Formula of anterior segments: $1 + S\frac{1}{1} + S\frac{1}{N}$. Dorsal cirri slightly pointed, as wide as high; ventral cirri not extending beyond the podial lobe.

Coloration of specimens after fixation yellowish brown, dorsal cirri reddish brown. Number of segments 120. Length 27 mm, width including the parapodia 1.3 mm.

Not represented in the ZIN collection.

Description after Imajima (1964).

Distribution. East of Japan, 37°55' N and 143°25' E; depth 2230–2350 m.

10. Genus EUMIDA Malmgren, 1865

(incl. Pirakia Bergström, 1914)

Cephalic lobe with 5 cephalic tentacles. One pair of usually large eyes. First segment reduced dorsally and fused with the 2nd segment. Four pairs of tentacular cirri, the first situated at the sides of the cephalic lobe; all tentacular cirri of the same form: spindle-shaped or slightly flattened. Setae present on 2nd and 3rd segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. Proboscis smooth, transversely wrinkled according to its compression, sometimes covered with small papillae. Parapodia uniramous. Setae segmented.

Type species: Eulalia sanguinea Oersted, 1843.

Eumida Malmgren is considered by some authors (Fauvel, 1923, and others) as a subgenus of Eulalia Savigny sensu lato, but it differs sharply in the reduction of the 1st segment. The genus contains about 10 species.

153 Key to species of the genus Eumida Malmgren

1 (10). Tentacular cirri cylindrical, spindle-shaped, pointed at the distal end.
2 (3). Dorsal cirri elongate, lanceolate, more than twice as long as wide; upper podial lip finger-shaped . . . . . 5. **E. fusigera** (Malmgren)
3 (2). Dorsal cirri heart-shaped and pointed, or oblong-oval, less than twice as long as wide; podial lips rounded.
4 (9). Dorsal cirri heart-shaped, with pointed distal end.
5 (8). Dorsal cirri slightly longer than wide.
6 (7). All segments of the same coloration . . . 1. **E. sanguinea** (Oersted)
7 (6). Two anterior segments not pigmented dorsally . . . . 2. **E. albopicta** (Marenzeller)
8 (5). Dorsal cirri as long as wide or slightly shorter than wide . . . . 3. **E. tubiformis** Moore
9 (4). Dorsal cirri oblong-oval, with rounded end . . . . 4. **E. minuta** (Ditlevsen)
10 (1). Tentacular cirri flattened, with distinctly, slender distal end . . . . 6. **E. nigrimaculata** (Moore)

1. **Eumida sanguinea** (Oersted, 1843) (Plate X, Figures 4, 5)

Oersted, 1843: 28, figs. 80, 82 (Eulalia); Malmgren, 1865: 97–98, pl. XIV, fig. 28; McIntosh, 1908: 66–70, pl. XLIII, figs. 9–10, pl. XLIV, fig. 4, pl. XLVIII, figs. 1–2, pl. LVIII, fig. 22, pl. LXVII, figs. 14–15; ? Izuka, 1912: 202, 203, pl. XXI, fig. 4; Bergström, 1914: 131–133, fig. 37; Deryugin, 1915: 332; Fauvel, 1923: 166–167, fig. 59, f–k (Eulalia (Eumida)); Augener, 1928: 708; Deryugin, 1928: 239; Zaks, 1933: 127; Annenkova, 1934: 322 (Eulalia); Fauvel, 1936: 58; Annenkova, 1937: 158;

1938 : 143 (*Eulalia* (*Eumida*)); Ushakov, 1939 : 83; Zatsepin, 1948 : 112, pl. XXIX, 10, b–d; Berkeley and Berkeley, 1948 : 47 – 48, fig. 69 (*Eulalia* (*Eumida*)); Ushakov, 1948a : 27; Vinogradov, 1949 : 47–48 (*Eulalia* (*Eumida*)); Okuda and Yamada, 1954 : 182 (*Eulalia* (*Eumida*)); Ushakov, 1950 : 169; 1955 : 98, fig. 6, D (*Eulalia* (*Eumida*)); Khlebovich, 1961 : 163 (*Eulalia* (*Eumida*)); Pettibone, 1963 : 88–89, fig. 21, a, b (synonymy); Imajima and Hartman, 1964 : 64–65, pl. 13, fig. e; Ushakov and Wu Pao-ling, 1965 : 153 (*Eulalia* (*Eumida*)); Levenshtein, 1966 : 8 (*Eulalia* (*Eumida*)); Buzhinskaya, 1967 : 80–81 (*Eulalia* (*Eumida*)).

Cephalic lobe rounded or slightly pointed anteriorly, with a slight depression at the posterior end, about as long as wide. Two large, black eyes in the posterior half of the cephalic lobe, and slightly before the eyes lateral to them there are sometimes small, dark spots (accessory eyes ?). Paired cephalic tentacles with pointed end and slightly widened at the base; median single tentacle larger than the paired tentacles and situated between the eyes or anterior to them. Proboscis smooth or slightly rugose (according to compression), partly covered with oblong, conical tubercles (papillae); 20–25 large marginal papillae at opening of proboscis (some of them bifid). All
154 tentacular cirri cylindrical, spindle-shaped, tapering to a pointed distal end, but the shortest ventral cirrus of the 2nd segment is sometimes markedly flattened. Dorsal tentacular cirri of 2nd and 3rd segments (if drawn posteriorly) reaching to the 11th–13th segment. Dorsal cirri on body segments in middle of body heart-shaped, slightly pointed, nearly symmetrical, with an incision at the base, slightly longer than wide; dorsal cirri in posterior part of body more elongate and pointed than in middle of body. Ventral cirri small, oval, slightly pointed, shorter than the podial process. Podial lobe with blunt, rounded upper and lower lip. Shaft of setae with spines at the end, distal part slightly serrate. Anal cirri spindle-shaped, pointed.

Coloration of body and dorsal cirri very variable, but mainly brown. Two color variations are known from the Sea of Japan (Zaks, 1933): var. *aurea*, with two dark transverse stripes at the anterior and posterior margin on the dorsal side of each segment in the anterior part of body, with unpigmented middle part of segments, and var. *olivacea*, in which a transverse, olive green stripe passes in the middle of each segment, the intersegmental surfaces lighter.

Number of segments 100–140. Length about 30 mm (maximum 60 mm), width 2–3 mm.

Mature specimens with eggs in the parapodia have been recorded from the Yellow Sea in May – July, near Southern Sakhalin and the Kuril Islands in August. Eggs greenish or reddish brown.

Distribution. The ZIN collection contains specimens from the Barents Sea (Murmansk), White Sea, southeast Kamchatka, Sea of Okhotsk, Sea of Japan, Yellow Sea, and from the Black Sea; they occur mainly in coastal areas to a depth of 30 m, among seaweed (120 specimens). Widely distributed, common in boreal regions; recorded from subtropical, tropical and antiboreal regions.

2. **Eumida albopicta** (Marenzeller, 1879) (Plate X, Figures 6, 7)

Marenzeller, 1879 : 128–129, pl. III, fig. 3, A–C (*Eulalia*); Izuka, 1912 : 207–208 (*Eulalia*); Fauvel, 1932 : 71 (*Eulalia*); Okuda, 1938 : 88, fig. 9

(Eulalia (Eumida) sanguinea); Fauvel, 1939: 275; 1953: 123, fig. 60, a, b (Eulalia); Imajima and Hartman, 1964: 64; Ushakov and Wu Pao-ling, 1965: 153 (Eulalia).

Cephalic lobe as in E. sanguinea. Proboscis markedly wrinkled in proximal part, with distinct transverse tubercles resembling ridges. Dorsal tentacular cirri of 2nd segment reaching to the 11th segment. Dorsal cirri oval-heart-shaped, with slightly pointed end, broader in anterior part of body and more elongate in posterior part. Ventral cirri oval.

Coloration gray with a reddish tinge; dorsal side darker than ventral side and cirri; first two segments without pigmentation. Characteristic for this species are light (white) spots on the dorsal side of the segments (1 or 2 on each segment); these spots are weakly marked in our specimen. About 80 segments. Length 18–20 mm, width 2–3 mm.

155 Mature females have been recorded from the Yellow Sea in May – June (Ushakov and Wu Pao-ling, 1965).

Remarks. This species closely resembles E. sanguinea (Oersted) and may be a color variant of it. The ZIN collection has one specimen.

Distribution. Southern coasts of Japan; Yellow Sea; coasts of Indo-China; Nicobar Islands.

3. **Eumida tubiformis** Moore, 1909 (Plate X, Figures 1–3)

Moore, 1909b: 342–344, pl. XVI, figs. 22, 23; Zaks, 1933: 127; Hartman, 1936a: 118; Annenkova, 1937: 158; 1938: 143–144 (Eulalia (Eumida)); Ushakov, 1955a: 99, fig. 6, A – C (Eulalia (Eumida)); Hartman and Barnard, 1960: 85; Khlebovich, 1961: 163 (Eulalia (Eumida)); Imajima, 1963: 352; Ushakov and Wu Pao-ling, 1965: 153–154 (Eulalia (Eumida)); Buzhinskaya, 1967: 81 (Eulalia (Eumida)).

Cephalic lobe slightly broader than long. Eyes with distinct hyaline lenses. Paired cephalic tentacles short and thick; lower pair slightly larger than the upper pair. Median single tentacle thinner and longer than the paired tentacles, situated between the eye spots or slightly anterior to the eyes. Proboscis smooth or slightly wrinkled (without distinct papillae); 30 soft, rounded, not completely bifid papillae at the outer margin; surface of papillae covered with conical tubercles. All tentacular cirri spindle-shaped and thick, with short, pointed end. Dorsal tentacular cirri of 2nd and 3rd segments (if drawn posteriorly) reaching to the 9th segment. Dorsal cirri on body segments large, broadly heart-shaped, with pointed apical part and a broad base, slightly asymmetrical; dorsal cirri wider than long, wider in anterior part of body, more elongate and pointed in posterior part. Cirrophores broad and low. Ventral cirri oval, with slightly pointed end, larger on the anterior segments than on the posterior segments. Rostrum of shaft of setae with small spines; distal part long and with finely denticulate margin.

Coloration of body and cirri dark brown, greenish brown or beige; darker spots or transverse stripes on the dorsal side of each segment, which extend from one parapodium to the next. To 135 segments. Length to 85 mm, width including the parapodia to 7 mm.

Mature females with numerous eggs in the parapodia and an everted proboscis have been recorded from the Sea of Japan, Tatar Strait and near Southern Sakhalin in August and September. Eggs reddish.

Remarks. This species differs from the closely related E. sanguinea in its shorter and broader dorsal cirri and in its darker coloration.

Distribution. The ZIN collection contains more than 25 specimens from the Sea of Japan (Peter the Great Bay, Tatar Strait), the southwestern part of the Sea of Okhotsk and the Kuril Islands; depth 2–80 m, ground: sand, gravel, shells. The species was described from California (depth 359–617 m).

156 4. **Eumida minuta** (Ditlevsen, 1917) (Plate XI, Figures 4, 5)

Ditlevsen, 1917 : 56, pl. IV, figs. 10, 12, 14 (Eulalia); Gorbunov, 1946 : 64 (Eulalia); Annenkova, 1946 : 185, 187, fig. 1, a – c (Eulalia arctica); Pettibone, 1954 : 238–239, fig. 27, c (synonymy).

Cephalic lobe rounded, as long as wide. Cephalic tentacles slender and long; single tentacle slightly larger than the paired tentacles, situated before the eyes. Pharynx not examined. First segment reduced dorsally, first pair of tentacular cirri situated at sides of cephalic lobe. Dorsal tentacular cirri with widened basal part and long, slender end (flask- or skittle-shaped); ventral tentacular cirri of 2nd segment shorter than dorsal cirri, with short, pointed end. Dorsal podial cirri oval; ventral cirri slightly larger than podial lobe. Podial lobe with two lips of different size. Shaft of setae widened at the end, distal part finely serrate.

Coloration of specimen in alcohol yellowish. Our specimen (incomplete): number of segments 20, length 3 mm, width 0.75 mm. According to Pettibone (1954), live specimens are reddish on the ventral side, greenish-reddish on the dorsal side. To 36 segments; maximum length (mature females) 8 mm.

Remarks. A specimen from the Novosibirskie Islands was compared with E. minuta (Ditlevsen) from the Point Barrow region (Chukchi Sea), collected by Pettibone, and no differences were found. The drawing of Annenkova (1946) is not quite correct; the 1st segment is reduced dorsally, so that one has to accept Pettibone's opinion (1954) that Eulalia arctica Annenkova, 1946 and Eulalia minuta Ditlevsen, 1917 are identical.

Wesenberg-Lund (1950a : 10) considers E. minuta Ditlevsen as a juvenile of E. bilineata Johnston, but they differ in the position of the single cephalic tentacle and in the form of the tentacular and podial cirri.

Distribution Recorded from the Arctic: Laptev Sea, Novosibirskie Islands, depth 45–65 m (Annenkova, 1946); Davis Strait, depth 122 m (Ditlevsen, 1917); Point Barrow region, depth 29–135 m (Pettibone, 1954). A specimen from the Novosibirskie Islands is in the ZIN collection.

5. **Eumida fusigera** (Malmgren, 1865) (Plate X, Figures 8–10)

Malmgren, 1865 : 100, pl. 14, fig. 27 (Sige); Levinsen, 1882 : 205; Bergström, 1914 : 136–138, fig. 40 (Sige macroceros, part.); Deryugin, 1915 : 331; Banse, 1959 : 424–425 (Eulalia); Eliason, 1962a : 18; Pettibone, 1963 : 90, fig. 21, e.

Cephalic lobe slightly pointed anteriorly, slightly wider than long. Median cephalic tentacle situated at level of eyes. Proboscis slightly widened distally, with a ring of 18 soft marginal papillae; proboscis covered with very 157 small papillae which form several regular longitudinal rows. Tentacular cirri spindle-shaped, cylindrical, with pointed distal end; dorsal tentacular cirrus of 2nd segment reaching to the 9th segment, ventral tentacular cirrus of 2nd segment the shortest, slightly flattened in the basal part. Setae present on 2nd segment. Dorsal cirri on body segments elongate and pointed, more than twice as long as wide. Ventral cirri also elongate, with pointed end. Podial lobe with long, finger-shaped upper lip and short, rounded lower lip.

Specimens preserved in alcohol are reddish brown on the cephalic lobe and on the dorsal side of the segments; there is a distinct transverse, pigmented stripe on each segment which is slightly narrower in the middle of the segments and wider at the base of the parapodia; dorsal cirri darker than the dorsal side of the body. Number of segments 45 (incomplete specimen). Length about 15 mm, proboscis 3 mm, width including the parapodia with setae 1.5 mm.

Described from the Oresund.

Remarks. Bergström (1914) considered *Sige fusigera* Malmgren, 1865 as a synonym of *Phyllodoce* (*Eulalia*) *macroceros* Grube, 1860, and gave the latter Malmgren's generic name *Sige*. Bergström stated that he reexamined Malmgren's specimen of *S. fusigera* in Stockholm, and found that the ventral cirrus on the 2nd segment was flattened, so that he doubted the accuracy of Malmgren's drawings. Banse (1959) concluded that *Pterocirrus macroceros* and *S. fusigera* are certainly distinct species, after a study of *Pterocirrus macroceros* from the Bay of Naples, from where the type of *P. macroceros* had been described. Banse placed *fusigera* in the subgenus *Sige*, and *macroceros* in the subgenus *Pterocirrus* (genus *Eulalia*). He did not examine *S. fusigera*, and did not mention the ventral cirrus of the 2nd segment; according to Banse, the two species differ distinctly in the position of the single median cephalic tentacle and in the form of the dorsal cirri.

The specimen described here, sent by Eliason, is from the Oresund, where Malmgren had also collected his material; it agrees well with the drawings of Malmgren. The ventral cirrus of the 2nd segment is not flattened but spindle-shaped, as in all other species of *Eumida*. Bergström's specimen may be damaged or wrongly labeled. Apart from the form of the ventral cirrus of the 2nd segment, *fusigera* differs from *macroceros* in the following characters: 1) setae present on 2nd and 3rd segments; 2) upper podial lip elongate (like a finger); 3) dorsal cirri lanceolate and elongate.

Distribution. Mediterranean (?), North Sea, coasts of Norway, Barents Sea, Massachusetts Bay.

6. **Eumida nigrimaculata** (Moore, 1909) (Plate XI, Figures 1–3)

Moore, 1909b: 344–346, pl. XVI, figs. 24–26 (*Eulalia*); E. Berkeley, 1924: 288 (*Eulalia*); Hartman, 1936: 117 (*Genetyllis*); Annenkova, 1938: 144 (*Eulalia* (*Eumida*)); Berkeley and Berkeley, 1948: 49 (*Eulalia*);

Ushakov, 1950: 169, pls. 1, 3 (Eulalia (Clavadoce) annenkovae); Ushakov, 1955a: 99–100, fig. 6, E, fig. 7, A–C (Eulalia (Eumida)); Buzhinskaya, 1967: 81 (Eulalia (Eumida)).

158 Cephalic lobe rounded, small tentacles. Eyes often with distinct hyaline lenses. Paired cephalic tentacles widely separated and situated much nearer to the posterior end of the cephalic lobe; single median tentacle slightly larger than the paired tentacles, situated at level of eyes; median single cephalic tentacle nearly as long as width of cephalic lobe. All cephalic tentacles are flask-shaped, with slender, pointed end. Proboscis covered with fine papillae; there are about 30 marginal papillae with small tubercles at the opening. All tentacular cirri distinctly flattened, broad, with small, slender, pointed end; if drawn posteriorly, they reach to the 8th or 9th segment (to the 12th segment according to Moore). Dorsal cirri of body segments in anterior part of body oblong-oval with rounded end; they are asymmetrical and their ends are long and pointed in the middle of the body. Dorsal cirri very large, especially on the anterior segments, where they cover the dorsal side of the body almost completely; they easily fall off and are not preserved after fixation (characteristic for this species). Ventral cirri broadly kidney-shaped and much larger than the podial process. Rostrum of shaft of setae with two denticles at the articulation covered with small spines, distal part finely denticulate.

Coloration: dorsal and ventral side of segments pale yellowish to reddish brown or dark gray with a bluish tinge; cephalic and podial appendages bright reddish or orange, usually darker than the dorsal side of the body. To 100 segments. Length to 60 mm, width including the parapodia to 5 mm.

Mature females with numerous dark eggs recorded from Southern Sakhalin in July – September.

Remarks. The form of the cephalic lobe with large paired cephalic tentacles, the fusion of the first two circumoral segments and the coloration of the dorsal cirri of Eumida nigrimaculata Moore make this species very similar to Genetyllis castanea (Marenzeller); but E. nigrimaculata differs in the presence of a median single cephalic tentacle. It is easy to confuse these two species if the material is damaged.

Bergström (1914: 165) stated that Eul. (Eumida) nigrimaculata Moore may represent a new genus, and Hartman (1936a: 117) placed it for some reason in the genus Genetyllis, which has no median single cephalic tentacle. The distinctly flattened (leaflike) tentacular cirri of Eul. (Eumida) nigrimaculata Moore resemble these of Clavadoce Hartman, 1936, but the 1st and 2nd segments of Clavadoce are completely reduced dorsally.

The specimens examined have tentacular cirri of markedly varying form; the drawing given here shows the broadest cirri, flattened to a maximum extent. Moore only stated that tentacular cirri of the anterior end are markedly flattened, but he did not give a drawing. The everted proboscis of one of our specimens shows that the proboscis is covered with numerous small, blunt, soft papillae of reticulate structure (see Plate XI, Figure 2). Moore also stated that the proboscis is covered with small, blunt, flat papillae; our specimens from the Far Eastern seas closely resemble those from American seas, but a more detailed comparison of the morphological characters is necessary.

Distribution. The ZIN collection contains specimens from the Sea of Japan (Peter the Great Bay, west coast of Southern Sakhalin), Sea of Okhotsk,
159 and the southern and northern Kuril Islands; depth 7–127 m (43 specimens). Recorded from Vancouver and the coast of California, Bay of Monterey, depth 129 m (Moore, 1909b; Berkeley and Berkeley, 1948).

11. Genus PTEROCIRRUS Claparède, 1868

Cephalic lobe with 5 tentacles. Eyes present or absent. First segment reduced dorsally and fused with the 2nd segment. Four pairs of tentacular cirri, ventral cirri of 2nd segment markedly flattened and with lateral fringes in the form of a sword or a knife. Setae present or absent on 2nd and 3rd segments. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$, $(1 + O\frac{1}{1}) + S\frac{1}{N}$ or $(1 + O\frac{1}{1}) + O\frac{1}{N}$. Proboscis diffusely covered with numerous papillae. Parapodia uniramous. Setae segmented.

Type species: Phyllodoce (Eulalia) macroceros Grube, 1860.

The genus contains about 10 species. Our collection contains 3 species, one of them new, Pt. imajimai. Imajima (1967) also recently described another new species from the coast of Japan, Pt. notoensis (Imajima), which has relatively short dorsal cirri and teat-shaped papillae on the proboscis. Banse and Hobson (1968) recently described Pt. parvoseta from Puget Sound, which also has very short papillae on the proboscis.

Remarks. Fauvel (1923) considered Pterocirrus as a subgenus of Eulalia Savigny sensu lato. Bergström suggested in 1914 placing species with modified tentacular cirri on the 2nd segment in the genus Sige Malmgren, wrongly considering Sige fusigera Malmgren, 1865 as a synonym of Ph. (Eulalia) macroceros Grube (see above). This was also done by Hartman (1959), who transferred all species described as Pterocirrus to the genus Sige Malmgren. However, Sige fusigera belongs to the genus Eumida Malmgren, 1865, as it has no flattened cirri on the 2nd segment which are characteristic for this group. Accordingly, all species with flattened cirri on the 2nd segment and a reduced 1st segment should be placed not in the genus Sige Malmgren but in the genus Pterocirrus Claparède, 1868, which was first used as a subgeneric name of Eulalia (Pterocirrus) velifera Claparède (= Phyllodoce (Eulalia) macroceros Grube).

Key to species of the genus Pterocirrus Claparède

1 (6). Dorsal cirri elongate, with pointed distal end, longer than wide.
2 (5). Single cephalic tentacle situated at anterior margin of cephalic lobe.
3 (4). Ventral cirri pointed . . . . 1. **P. macroceros** (Grube)
4 (3). Ventral cirri bean-shaped . . . . 2. **P. slastnikovi** Annenkova
5 (2). Single cephalic tentacle situated at posterior margin of cephalic lobe . . . . 4. **P. imajimai** Uschakov
6 (1). Dorsal cirri heart-shaped, as long as wide . . . . 3. **P. notoensis** (Imajima)

160 1. Pterocirrus macroceros (Grube, 1860) (Plate XI, Figures 6–9)

Grube, 1860: 82, pl. III, fig. 4 (Phyllodoce (Eulalia)); Claparède, 1868: 250–252, pl. XVII, fig. 2 (Eulalia (Pterocirrus) velifera); Bergström, 1914: 136–137, fig. 40 (Sige, part.); Fauvel, 1923: 167–168, fig. 60, d–g (Eulalia (Pterocirrus), part.); ? Berkeley and Berkeley, 1948: 48, fig. 70 (Eulalia (Sige)); Vinogradov, 1949: 32–33 (Eulalia (Pterocirrus)); Ushakov, 1955a: 100 (Eulalia (Pterocirrus)); Banse, 1959: 423–426, fig. 2 (Eulalia (Pterocirrus)); Ushakov and Wu Pao-ling, 1965: 154, fig. 1, G–I (Eulalia (Pterocirrus)); Day, 1967: 152, fig. 5, 4, a–c (Eulalia (Pterocirrus)); Banse and Nichols, 1968: 223–225, fig. 1, a–c (Eulalia (Pterocirrus)).

Cephalic lobe rounded, about as long as wide. Two very large, oblong, dark eyes at sides of cephalic lobe. Cephalic tentacles longer than cephalic lobe, threadlike, with pointed end; median single tentacle the largest, situated before the eyes, at the level of the paired tentacles at the anterior margin of the cephalic lobe. Proboscis densely covered with numerous long, teat-shaped papillae ("shaggy"). First circumoral segment markedly reduced on the dorsal side; next two segments fully developed. Ventral tentacular cirri of 2nd segment leaf-shaped (with a lateral fringe like a sword); other tentacular cirri threadlike or spindle-shaped, dorsal cirri of 2nd segment the longest. Setae absent on 2nd and 3rd segments. Formula of anterior segments: $(1 + O\frac{1}{1}) + O\frac{1}{N}$.

Dorsal cirri in middle of body lanceolate, elongate, with pointed distal end; ventral cirri of the same form but markedly smaller. Podial setigerous lobe divided, the upper lip slightly larger than the lower. Shaft of setae slightly widened and serrate at the distal end; distal part of setae elongate, serrate.

Coloration grayish green, dorsal side slightly darker than ventral side and dorsal cirri. There is sometimes a characteristic triangular spot on the cephalic lobe, between the eyes. All our specimens are small: number of segments 65–70, length 15–18 mm, width 1 mm.

Remarks. Bergström (1914) gave the following formula for Pt. macroceros: $1 + S\frac{1}{1} + S\frac{1}{N}$. However, Banse (1959) proved that setae on the 2nd and 3rd segments of Pt. macroceros are absent, and this was continued by Day (1967) for this species from the coast of Africa. Our specimens from the Black Sea agree with Banse's data: there are no setae on the anterior segments, but some had acicula on the 3rd segment (not mentioned by Banse). Pt. macroceros from the Black Sea and Banse's specimen from the Mediterranean are apparently identical.

Imajima and Hartman (1964) described a variety of this species, orientalis (2 specimens) from the coast of Japan (Hokkaido). It differs from the type form in having setae on the 3rd segment (the authors state that this variety differs from the type form in having no setae on the 2nd segment, since they accepted the formula of the type form given by Bergström). Four
161 specimens of Pt. macroceros from Hainan Island, the Yellow Sea and Pos'et Bay in the Sea of Japan (the Pos'et Bay specimen in good condition), which we examined had no setae on the 3rd segment; the type form and the variety described above possibly occur in the Northwest Pacific.

Distribution. Twelve specimens in the ZIN collection are from the Black Sea, Hainan Island and Pos'et Bay in the Sea of Japan. Recorded also from the Atlantic coast of Europe, the Mediterranean and the Pacific coast of Canada.

2. **Pterocirrus slastnikovi** Annenkova, 1946 (Plate XII, Figures 6–11)

Annenkova, 1946: 186, 188, fig. 2 (Eulalia (Pterocirrus)).

Cephalic lobe conical, markedly widened at the base and blunt anteriorly, slightly wider than long. Eyes absent, but there are 2 large, oblong, dark spots on the dorsal side of the cephalic lobe, imitating eyes. Median single cephalic tentacle and upper paired tentacles long and slender; lower paired cephalic tentacles shorter and thicker than the upper. Median single cephalic tentacle situated near anterior margin of cephalic lobe, longer than the cephalic lobe. Proboscis with long numerous papillae ("shaggy"). Tentacular cirri, except the ventral cirri on the 2nd segment, with widened base and elongate end, ventral tentacular cirri of 2nd segment very large, leaf-shaped, flattened, slightly asymmetrical and with pointed end. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$ (see Remarks). Dorsal cirri of body segments in middle of body lanceolate, with short, pointed end; they are slightly shorter on the anterior segments. Ventral cirri flattened, bean-shaped, covering the posterior side of the podial lobe. Podial lobe with two rounded lips, upper lip slightly longer than lower lip. Setae long, terminal widening of the shaft with thin spines; distal part elongate, slender and distinctly denticulate.

Dorsal side of body dark olive green, ventral side yellowish. Number of segments 34–40. Body short and broad, its anterior end blunt and distinctly broader than the posterior end; length to 10 mm, width to 2 mm.

Remarks. Annenkova (1946) stated that setae are present on the 2nd segment, but reexamination of my material proved that there are no setae on the 2nd segment, but setae are present on the 3rd segment (specimens in bad condition).

Distribution. Laptev Sea, depth 22–869 m, ground sandy silt (3 specimens).

3. **Pterocirrus notoensis** (Imajima, 1967) (Plate XII, Figure 5)

Imajima, 1967: 411–412, fig. 3 (Sige).

Cephalic lobe rounded, with a slight depression at the posterior end; cephalic lobe wider than long. Two large eyes. Cephalic tentacles large,
162 with pointed distal end, longer than the cephalic lobe; median single cephalic tentacle situated at level of eyes at posterior margin of cephalic lobe. Proboscis densely covered with teat-shaped papillae; distal end of proboscis with 17 large, rounded papillae. First segment reduced on the dorsal side, next two segments fully developed. Ventral tentacular cirri of 2nd segment flattened, with a lateral fringe. Setae present on 2nd and 3rd segments. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. Dorsal cirri of all body

segments heart-shaped, with pointed end, as long as wide; ventral cirri oval. Podial lobe rounded, with a small incision. Rostrum of setae with small spines; distal part finely serrate.

Coloration of specimens in alcohol yellowish brown; small brown spots on dorsal side of body and on the dorsal cirri. Number of segments 44. Length 6 mm, width including the parapodia 1 mm.

Not represented in the ZIN collection.

Description after Imajima (1967).

Distribution. West coast of Japan, Noto peninsula, littoral zone.

4. **Pterocirrus imajimai** Uschakov, n. sp. (Plate IX, Figures 11–14)

Cephalic lobe rounded, about as wide as long; 2 small depressions at anterior and posterior end. Two large pigmented spots, imitating eyes, in anterior part of cephalic lobe; two semicircular pigmented stripes at posterior end. Frontal cephalic tentacles very large, with pointed distal end; single cephalic tentacle long, slender, situated at posterior margin of cephalic lobe. Proboscis densely covered with threadlike papillae. Ventral tentacular cirri of 2nd segment (V_{II}) flattened, typical for Pterocirrus. First segment not recognizable on the dorsal side. Setae present on 2nd segment. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. Parapodia with high cirrophores for the dorsal cirri, which are elongate with slender, pointed end. Podial lobe large, with two lips of different size, upper lip larger. Ventral cirrus slender and pointed. Setae with serrate distal part; 20–25 setae in a bundle.

Our collection contains only 2 incomplete specimens: 32 segments are preserved on the larger fragment. Length 6 mm, width including the parapodia and setae 2 mm.

The species is named after Imajima, who described numerous abyssal polychaetes from the Northwest Pacific (Imajima, 1964).

Type deposited at ZIN AN SSSR, No. 1/16273.

Remarks. The species resembles Pt. slastnikovi Ann. in the "shaggy" type of proboscis and in the two large pigmented spots imitating eyes on the cephalic lobe; however, it differs from this species in the position of the median cephalic tentacle, which is situated at the posterior margin of the cephalic lobe, not at the anterior end, as in Pt. slastnikovi. The ventral cirri of the parapodia are also small, while they are very large and completely cover the podial lobe in Pt. slastnikovi.

163 Distribution. East of Honshu – 38° N and 146°30' E, depth 5460 m, silt ("Vityaz," station 3575, 1957, one specimen); coast of California – 24°58' N and 113°25' W, depth 3260 m, silt ("Vityaz," station 4265, 1959, type).

12. Genus **AUSTROPHYLLUM** Bergström, 1914

Cephalic lobe square, with rounded corners. Five cephalic tentacles; median single cephalic tentacle situated at posterior margin of cephalic lobe. Eyes absent. Proboscis with diffuse, soft papillae in proximal part; the papillae form 6 longitudinal stripes in the distal part of the proboscis. First tentacular segment partly reduced dorsally, covered by the cephalic lobe. Four pairs of tentacular cirri: $1 + S\frac{1}{1} + S\frac{1}{N}$. Parapodia pseudobiramous (with 2 acicula), the accessory aciculum situated at the base of the dorsal cirrus; there are sometimes 1 or 2 hairlike setae near this aciculum on the anterior segments; podial lobe with segmented setae. Dorsal cirri oblong-oval or irregularly heart-shaped.

Type species — Eulalia charcoti Gravier, 1911.

This genus was until recently considered as monotypic. Hartman (1964) included in it specimens from the Antarctic, described by Monro (1930) as Phyllodoce longipes Kinberg, 1866, and named them Austrophyllum monroi Hartman, 1964, because their parapodia have 2 acicula. However, as our material from the Antarctic (Averintsev, 1972) has shown, the form of the cephalic lobe, i.e. absence of a median cephalic tentacle, prevents its inclusion in the genus Austrophyllum, and because of the structure of the proboscis, this species should form a separate genus, Zverlinum Averincev.

The ZIN collection contains specimens of A. charcoti (Gravier, 1911) from the Antarctic ("Ob" expedition) and 2 specimens of A. sphaerocephala (Levenshtein, 1961) collected at great depths near the Kuril Islands, which closely resemble A. charcoti in the structure of the cephalic lobe and of the proboscis, but differ from it because sphaerocephala has hairlike setae near the dorsal cirrus. I place in this genus also Notophyllum caecum Fauvel, 1913, described from the Azores (depth 5000 m), because its proboscis has 6 stripes of flattened papillae in the distal part and its median cephalic tentacle is situated at the posterior margin of the cephalic lobe, which is characteristic for Austrophyllum, while the occipital nuchal organs, considered as a main character of Notophyllum, are absent in N. caecum. A notopodial aciculum and an accessory notopodial seta are present in N. caecum Fauvel only from the 20th to the 25th setose segment, while they are present on the first segments in Austrophyllum; however, this character is probably of secondary importance.

Key to species of the genus Austrophyllum Bergström, 1914

1 (2). One or 2 notopodial hairlike setae at base of dorsal cirrus. Dorsal cirrus with a single median vein . . . . 1. **A. sphaerocephala** (Levenstein)
164 2 (1). Notopodial hairlike setae absent. Dorsal cirrus with branched venation . . . . ***A. charcoti** (Gravier, 1911)
Antarctic

1. **Austrophyllum sphaerocephala** (Levenstein, 1961) (Plate XIII, Figures 1—4)

Levenshtein, 1961 : 150—151, fig. 2; 1965 : 8 (Eulalia).

Cephalic lobe characteristic for the genus Austrophyllum: paired cephalic tentacles situated at anterior margin, median single cephalic tentacle at posterior margin of cephalic lobe. Paired cephalic tentacles slightly widened at the base, with pointed end, median unpaired tentacle threadlike and slightly longer than cephalic lobe. Posterior margin of cephalic lobe straight, smooth, weakly rounded, slightly overlapping the first tentacular segment; occipital processes absent. Proboscis retracted in our specimens, but it is seen in preparations that the papillae are arranged diffusely in the proximal part of the proboscis, but form 6 broad longitudinal stripes in the distal parts; papillae of this species of about the same form as in A. charcoti (Gravier), i.e. broadly oval, leaf-shaped, with large gland cells at the outer margin; proximal part of proboscis about as long as its distal part (distal part almost 7 times as long as the proximal part in A. charcoti); distinct marginal (oral) papillae absent at distal end of proboscis, it is only slightly undulant. Tentacular cirri long, threadlike, with pointed end: first pair (on 1st segment), if drawn posteriorly, reaching to the 8th or 9th segment, second pair (dorsal cirri on 2nd segment) reaching to the 15th segment, third pair (ventral cirri on 2nd segment) reaching to the 6th segment, fourth pair to the 15th segment. On the parapodia in the middle of the body, there are, in addition to the notopodial acicula, 1 or 2 hairlike setae at the base of the dorsal cirrus which are directed outward. Dorsal cirri of anterior segments more elongate than on the middle segments and more or less regularly oblong-oval; anterior dorsal cirri about twice as long as wide; dorsal cirri of middle segments elongate, irregularly heart-shaped; there is a weak yellow vein in the median line of the dorsal cirri; dorsal cirri with numerous oblong gland cells. Ventral podial cirri with pointed end, larger than the podial lobe; their distal end directed upward. Podial lobe short, thick, upper and lower lips of the same size. Setae numerous, with slender, long end part with weakly denticulate margin; the slightly widened distal part of the shaft (rostrum) slightly spinose. Anal cirri long. Segments with distinct secondary annulation.

Dorsal and ventral side dark gray with a greenish tinge; podial appendages darker; some dorsal cirri with dark dots in upper part (coloration of our larger specimen lighter). About 125 and 170 segments (last segments very small and difficult to count). Length 30 and 70 mm, width 3 and 3.5 mm.

165 Remarks. The description is based on 2 specimens from the Kuril-Kamchatka Trench (ZIN AN SSSR, No. 1/2263). Our specimens are identical with Eulalia sphaerocephala Levenstein, 1961, from the Bering Sea in the characteristic form of the cephalic lobe. Levenshtein gave only a very short diagnosis; she did not describe the proboscis and did not state whether there is an accessory notopodial aciculum, but this has been proved to be present by reexamination of her specimens.

This species differs from A. charcoti (Gravier), in addition to the presence of notopodial setae, in its smaller size; but the number of segments is the same in both species.

Distribution. Bering Sea — western basin, depth 2440 and 3680 m, ground — diatomite-clay silt; 2 specimens (Levenshtein, 1961); Kuril-Kamchatka Trench, depth 3800–4130 m ("Vityaz," 1953, station 2209, 2 specimens).

13. Genus **VITIAZIA** Uschakov, 1953

Cephalic lobe broadly triangular, with 4 frontal cephalic tentacles; there is a rounded papilla in the middle of the dorsal side (underdeveloped median cephalic tentacle). Behind the cephalic lobe are 2 occipital organs (like the epaulets of Notophyllum Oersted). Eyes absent. Proboscis smooth, with large marginal (oral) papillae. All three anterior tentacular segments are separated and fully developed. Four pairs of tentacular cirri. Formula of anterior segments: $1 + S\frac{1}{1} + \frac{1}{N}$. Parapodia uniramous; podial lobe conical, with large upper lip ending in an elongate finger-shaped process. Setae all complex (segmented).

The genus contains only one species — Vitiazia dogieli Uschakov, 1953 (type species).

1. **Vitiazia dogieli** Uschakov, 1953 (Plate XIV, Figures 1—4)

Ushakov, 1953: 207—208, fig. 1, A—C; 1955a: 96, fig. 4, D—F.

Cephalic lobe slightly broader than long; frontal cephalic tentacles small, situated close together at anterior margin of cephalic lobe. In a strongly macerated specimen there were two small pigmented dots near the posterior end, possibly a remnant of eye spots. Occipital organs (epaulets) semicircular, weakly pigmented, extending onto the first segment. Proboscis thick, with smooth or wrinkled surface, according to compression, with 16—18 rounded outer marginal papillae, with microscopic tubercles. First tentacular segment very large, broader than the cephalic lobe. Lower cirri of 2nd segment slightly flattened, all other cirri cylindrical; first pair of cirri and lower cirri of 2nd segment markedly shorter than upper cirri of 2nd segment and cirri of 3rd segment; the longest tentacular cirri reach to the 7th segment. Tentacular cirri of 2nd segment widely separated; podial lobe with small, complex setae, near the ventral cirrus. Form and size of
166 dorsal cirri on body segments varying: they may be lanceolate or very short, not longer than wide. Ventral cirri large, pointed, slightly longer than the podial lobe. Its anterior lobe is bifid, the upper lip much larger than the lower and with a long, finger-shaped process. One very long aciculum. Fifty or more setae on one parapodium; their rostrum is slightly widened, denticle at articulation with numerous small spines; distal part slender, long, with indistinct fine denticulation.

Coloration grayish beige, with weak punctate pigmentation; dorsal side slightly darker than ventral; dorsal and ventral cirri usually with weak punctate pigmentation. To 65 segments; length over 50 mm (specimen incomplete), width including the parapodia to 8 mm; proboscis 15 mm long, 4 mm wide.

Type deposited at ZIN AN SSSR, No. 2/15833 ("Vityaz," station 5616).

Remarks. V. dogieli was described from a single specimen (Ushakov, 1953). Levinshtein sent me 5 specimens in much better condition which had been collected in the same area and at the same depths as the first specimen. This made it possible to amend the original description in some points. I had considered the rounded papilla in the middle of the cephalic lobe as a remnant of a single median tentacle, but there was at this point a short papilla in all other specimens, which should be considered a developing tentacle; in other genera with occipital epaulets, a median normal cephalic tentacle is present. The new specimens showed marked variation in the form of the parapodia and of the dorsal cirrus.

The elongate form of the parapodia, illustrated in the description of the first specimen, is not quite normal (as is confirmed by the position of the aciculum); more typical, short parapodia are shown on Plate XIV, Figure 3 in this work. Regardless of the length of the parapodia, an elongate finger-shaped process on the upper lip is characteristic for this species. The variation in form of the dorsal cirrus, not only in different specimens but even in the same specimen, is apparently a specific character. One specimen had a cirrus in the middle of the body which was twice as long as the other cirri. The form of the parapodia in this abyssal species has apparently not become stabilized.

Distribution. Northwest Pacific, southeast of the Kuril Islands and Tsugaru Strait, depth 6157–8100 m (6 specimens).

14. Genus **VITIAZIPHYLLUM** Uschakov, n.gen.

Cephalic lobe slightly tapering anteriorly, much wider posteriorly. Five cephalic tentacles. Eyes absent. Two nuchal organs (epaulets) at posterior margin of cephalic lobe. Proboscis smooth, with rounded marginal (oral) papillae. First segment reduced dorsally. Four pairs of spindle-shaped tentacular cirri: $(1 + S\frac{1}{1}) + S\frac{1}{N}$. Parapodia uniramous. Dorsal cirri pointed, lanceolate.

167 Type species – V. nuchalum Uschakov.

Remarks. Paired nuchal organs are present only in Notophyllum Oersted, Nipponophyllum Imajima and Hartman, Hesperophyllum Chamberlain, Vitiazia Uschakov, and in the new genus Vitiaziphyllum. The genus Hesperophyllum, described from the coast of California (Chamberlin, 1919a), differs from Notophyllum mainly in the flattened ventral cirrus of the 2nd segment; the diagnosis of this genus is very incomplete and the description of the single species is not accompanied by drawings (Hesperophyllum and Notophyllum may be identical). The three anterior segments of Vitiazia are fully developed and distinctly separated and the parapodia are uniramous. The 1st segment of Vitiaziphyllum is reduced on the dorsal side, and the parapodia are also uniramous. The two anterior segments of Notophyllum and Nipponophyllum are fused on the dorsal side and reduced (partly or completely), and the parapodia are biramous. There thus seems to be a straight series of complication of the anterior end and parapodia: Vitiazia–Vitiaziphyllum–Notophyllum and Nipponophyllum.

1. **Vitiaziphyllum nuchalum** Uschakov, n.sp. (Plate XV, Figures 1–3)

Cephalic lobe conical. Frontal cephalic tentacle large, tapering distally, only slightly shorter than maximum width of cephalic lobe; median cephalic tentacle slender, long, situated at posterior margin of cephalic lobe. One pair of broad, short, rounded nuchal organs. Proboscis long (about as long as 20–25 body segments), strongly tuberculate-wrinkled (probably due to incomplete eversion), with about 20 rounded marginal papillae at the oral end. First segment indistinguishable dorsally; 1st pair of tentacular cirri situated at sides of cephalic lobe (cirri lost). Second segment normal; ventral tentacular cirri only half as long as the dorsal cirri, which reach to the 15th segment; tentacular cirri cylindrical. Setae present near the tentacular cirri on the 2nd segment. Cirrophores of dorsal cirri on all body segments very large, distinctly separated. The dorsal cirrus was present only on one segment in the middle of the body; it is slightly longer than the podial lobe, lanceolate and pointed. Podial lobe thick, with a very large, long aciculum. Ventral cirrus long and slender, pointed, longer than the podial lobe. Posterior segments lost. About 15 setae in a bundle, their distal part slender, long, slightly denticulate, rostrum with double denticulate margin.

Coloration uniformly pale beige. Forty segments (incomplete specimen). Length 7 mm, width including the podial lobe (without setae) 1.5 mm, length of proboscis 2 mm.

Two specimens.

Type deposited at ZIN AN SSSR, No. 1/16439.

Distribution. East of Honshu – 38°02' N and 146°33' E, depth 5475 m (type); Northeast Pacific – 48°21' N and 144°16' W, depth 3704 m (cotype).

168 15. Genus **NOTOPHYLLUM** Oersted, 1843

Cephalic lobe rounded, with 5 cephalic tentacles. Occipital (nuchal) organs resembling epaulets, situated at posterior margin of cephalic lobe. One pair of large eyes. Proboscis with lateral longitudinal rows of leaf-shaped papillae.

One or two first segments reduced dorsally. Four pairs of elongate spindle-shaped tentacular cirri. Formula of anterior segments: $(1 + S\frac{1}{1}) + S\frac{1}{N}$.

Parapodia pseudobiramous, i.e. with 2 acicula; there may be one or several hairlike setae near the notopodial cirrus. Podial lobe with numerous segmented setae. Dorsal cirri large, broadly oval (kidney-shaped), overlapping like tiles, nearly completely covering the dorsal side of the body; Notophyllum resembles in this respect the genus Paranaitis Southern (p. 133).

Type species: Phyllodoce foliosa M. Sars, 1835.

Species of Notophyllum deposit eggs from the dorsal side, where they pass the first stages of development protected by the dorsal cirri (Okada, 1930; Buzhinskaya, 1967), as in some Polynoidae under the protection of the dorsal scales.

The genus contains about 6 species. In our collection are only 2 species from northern and Far Eastern seas: N. foliosum (M. Sars) and N. imbricatum Moore. N. splendens (Schmarda), recorded from the Yellow Sea (Ushakov and Wu Pao-ling, 1965) is in the collection of the Institute of Oceanology of the Academy of Sciences of China (Tsingtao), but needs a more detailed description. The synonymy of the last species is confused. Augener (1913 : 140) and Fauvel (1930 : 515) consider N. multicirris Grube, 1878, from the Philippines, as a synonym of N. splendens. Grube shows some warts (?) on the dorsal cirri of N. multicirris; these may represent large gland cells, but neither Augener nor Fauvel mentions these formations. Fauvel (1953) also considers N. imbricatum Moore, 1906, as a synonym of N. splendens, but we think that this is not correct.

According to Day (1953, 1967), N. splendens (Schmarda) has no hairlike setae near the notopodial aciculum, which was not mentioned by earlier authors; such setae are present in N. imbricatum (see below).

Key to species of the genus Notophyllum Oersted

1 (2). Nuchal organ forming a pair of short, rounded or bifid processes . . . . 1. **N. foliosum** (M. Sars)
2 (1). Nuchal organ consisting of 2–4 or more pairs of elongate processes.
3 (4). Notopodial aciculum accompanied by 1 or 2 hairlike setae . . . . 2. **N. imbricatum** Moore
4 (3). Notopodial aciculum without hairlike setae . . . . **N. splendens** (Schmarda), 1861

Day, 1967 : 151, fig. 5, 3, k–n.
South Africa, Red Sea, coast of India, Ceylon, Philippines, Yellow Sea, New Caledonia, southwest coast of Australia

169 1. **Notophyllum foliosum** (M. Sars, 1835) (Plate XIII, Figure 10)

Malmgren, 1865 : 93, pl. XIV, fig. 33 (N. polynoides); Levinsen, 1882 : 209–211, pl. VII, figs. 1–3 (Trachelophyllum lütkeni); McIntosh, 1908 : 46–50, pl. XLV, fig. 1, pl. XLVII, fig. 21 (synonymy); Bergström, 1914 : 120–123, textfig. 31 (synonymy); Fauvel, 1923 : 170–171, fig. 61, a–e; 1933 : 16; Hartman, 1948a : 18, fig. 3, d–f; Wesenberg-Lund, 1950a : 10, map 14, pl. I, fig. 4; Ushakov, 1955a : 95; Pettibone, 1963 : 83–84, fig. 17e; Guy, 1964 : 181; Ushakov and Wu Pao-ling, 1965 : 151, fig. 1, 8.

Cephalic lobe rounded anteriorly. Eyes often with distinct lenses. Cephalic tentacles large, spindle-shaped or slightly flattened, tapering distally; single cephalic tentacle much larger and longer than the paired tentacles, situated at level of eyes. One pair of short, rounded, rarely bifid, occipital processes at posterior margin of cephalic lobe. Only 1st segment reduced dorsally. Tentacular cirri of the same form as the cephalic tentacles but larger. Dorsal tentacular cirri of 2nd and 3rd segments the longest, if drawn posteriorly, they reach to the 9th or 10th segment. Dorsal cirri on body segments very large, thick, twice as wide as long, their inner margin strongly extended. Outer margin with numerous oblong gland cells. Ventral cirri transverse-oval, much larger than the podial lobe. At the base of dorsal cirrus is an aciculum and 1 or 2 hairlike setae. Ventral podial lobe with numerous segmented setae. Rostrum of shaft of setae with large, pointed spines; distal part saber-shaped finely serrate.

Coloration of specimens in alcohol mainly brown, and there are dark spots on the outer margin of the dorsal cirri.

To 115 segments. Length 50–60 mm, width including the parapodia 5 mm (specimens from Far Eastern seas are not longer than 20 mm).

Remarks. Fauvel (1933) considers N. japonicum Marenzeller, 1879 (Izuka, 1912) as a synonym of N. foliosum (M. Sars), but Imajima and Hartman (1964) redescribed N. japonicum and placed it in the new genus Nipponophyllum (p. 171).

The bifid nuchal organs of N. foliosum are illustrated by Wesenberg-Lund (1950a, pl. I, fig. 4) in a specimen from the Norway Sea; similar nuchal organs are present in specimens from the Yellow Sea and Bering Island (see Plate XIII, Figure 10).

Distribution. Occurs in the Yellow Sea (Tsingtao, littoral zone), Sea of Japan (Peter the Great Bay), near the Kuril Islands, Bering Island; depth 0—52 m (11 specimens). Recorded from the Atlantic Ocean, east coast of North America (Chesapeake Bay), Faeroes, Atlantic coast of Europe; Mediterranean; west coast of Africa. There are isolated records from the Pacific, Yellow Sea (Fauvel, 1933), Gulf of Alaska (Hartman, 1948a); depth to 1750 m.

170 2. **Notophyllum imbricatum** Moore, 1906 (Plate XIII, Figures 5—9)

Moore, 1906 : 217—219, pl. X, figs. 1—3; 1908 : 329; Berkeley, 1924 : 287; Annenkova, 1934 : 322; Fauvel, 1936 : 59; Annenkova, 1937 : 159; 1938 : 146 (nec Okuda, 1939 : 227, fig. 4); Hartman, 1948a : 18, fig. 3, a—c; Berkeley and Berkeley, 1948 : 42—43, figs. 60—61; Ushakov, 1955a : 95, fig. 4, A—C; ?Knox, 1960 : 113—114, figs. 141—142; Ushakov and Wu Pao-ling, 1965 : 152; Buzhinskaya, 1967 : 80.

Cephalic lobe rounded or slightly conical anteriorly, its posterior part often with a distinct swelling like a semicircular cushion, which partly covers the eyes and is the base for the median single cephalic tentacle. Eyes, cephalic appendages and tentacular cirri as in N. foliosum. Nuchal processes situated at posterior margin of cephalic lobe; they are divided into 3, more rarely 4 or more parts of different size. The anterior segments are usually partly reduced dorsally and fused. Pharynx retracted in most specimens examined, partly everted only in two specimens; proximal part of proboscis smooth, but there are two lateral longitudinal rows of papillae some distance from the proximal end which are small, but become gradually larger and longer, and more numerous in each row; anterior part of proboscis covered throughout with numerous large papillae; large lateral papillae and the "smooth" surface of the proboscis densely covered with very small spherical formations with finely granulate surface (visible only under high magnification; dorsal side also with transverse folds. The proboscis resembles to some extent that of the subgenus Mysta (genus Eteone) (convergence in unrelated genera of Phyllodocidae). Dorsal cirri of body segments broad, kidney-shaped, overlapping like tiles, almost entirely covering the dorsal side; the outer margin of the dorsal cirri becomes weakly undulate (goffered) in fixed specimens; ventral cirri broadly oval (ventral and dorsal cirri as in N. foliosum). There is a small tubercle with an aciculum and usually with 2 or 3 short, hairlike setae at the base of the dorsal cirrus. Ventral part of parapodia with 40 or more segmented setae.

Coloration grayish olive or brownish; dorsal and ventral cirri dark olive or greenish brown, usually darker than the dorsal surface.

To 125 segments, length to 75 mm, width including the parapodia and the setae 7—8 mm.

Remarks. Notophyllum imbricatum Moore, 1906 resembles N. americanum Verrill, 1885, described from the Massachusetts area, but the nuchal occipital organs of this species have 4–7 processes (Pettibone, 1963). These 2 forms may be subspecies, but a detailed comparison of specimens is necessary.

Distribution. Our records: Yellow Sea, Sea of Japan, La Pérouse Strait, Aniva Bay, Kuril and Komandorski Islands; depth 0–75 m, mainly
171 on pebbly ground (62 specimens). Recorded also from the Gulf of Alaska, Vancouver and the coast of California; recorded from the New Zealand region (Knox, 1960).

16. Genus **NIPPONOPHYLLUM** Imajima and Hartman, 1964

Cephalic lobe with 5 tentacles. One pair of large eyes. Paired occipital (nuchal) organs situated at posterior margin of cephalic lobe. Three anterior segments reduced dorsally and fused. Four pairs of tentacular cirri. Proboscis with soft papillae. Parapodia pseudobiramous; there are hairlike setae near the notopodial aciculum. Ventral podial lobe with numerous segmented setae.

Type species: Notophyllum japonicum Marenzeller, 1879.

This genus is closely related to Notophyllum Oersted, but Imajima and Hartman state that the arrangement of the tentacular cirri is unusual: $S\frac{1}{1} + S\frac{1}{1}$. A different interpretation of the arrangement of the peristomal cirri is possible: as in other closely related genera, this genus may have 3 segments with tentacular cirri, but these segments have become fused, with reduction of the neuropodia of the 3rd segment. As a result, all the tentacular cirri became situated close together, so that 2 of them seem to be situated on the 1st segment. If this is correct, the formula of the anterior segments would be: $(1 + S\frac{1}{1} + S\frac{1}{O})$, and the following segments would be normal. However, this can only be determined by sections.

According to Imajima and Hartman, this genus contains only two species.

Key to species of the genus Nipponophyllum Imajima and Hartman

1 (2). Occipital organ consisting of 2 pairs of processes . . . . 1. **N. japonicum** (Marenzeller)
2 (1). Occipital organ consisting of 4 pairs of processes . . . . 2. **N. sagamianum** (Izuka)

1. **Nipponophyllum japonicum** (Marenzeller, 1879)

Marenzeller, 1879: 126–127, pl. 3, fig. 1 (Notophyllum); Izuka, 1912: 200–210 (Notophyllum); Fauvel, 1936: 59 (Notophyllum); Okuda, 1939: 227, textfig. 4 (Notophyllum imbricatum); Imajima and Hartman, 1964: 67–68, pl. 14, figs. a, b.

Cephalic lobe rounded anteriorly; its posterior median part slightly concave. Eyes situated in broadest part of posterior part of cephalic lobe.

Paired cephalic tentacles situated slightly ventrally; median single cephalic tentacle situated at level of eyes, 3/4 as long as the cephalic lobe. Proboscis entirely covered with papillae. Occipital organ consisting of 2 pairs of nuchal processes, the outer processes about twice as long as the inner. Anterior segments fused. Tentacular cirri cylindrical, with pointed end.
172 Dorsal cirri on body segments large, bean-shaped, overlapping. Each notopodium with a hairlike seta projecting outward above the aciculum. Ventral podial lobe with a small incision at the distal end and with a bundle of segmented setae (12—18). Distal part of setae finely serrate; rostrum of shaft of setae with spines.

Coloration yellowish brown. To 70 segments; length to 15 mm, width 2.5 mm.

Description after Imajima and Hartman (1964); not represented in our collection.

Distribution. Coasts of Japan, Hakodate, Sagami Bay, Onagawa, southern Japan.

2. **Nippophyllum sagamianum** (Izuka, 1912)

Izuka, 1912 : 210—211, pl. XXI, figs. 7—9 (Notophyllum); Imajima and Hartman, 1964 : 68.

Cephalic lobe oblong, pentagonal. Lateral-anterior margin of lobe slightly concave. Eyes large, oval. Frontal cephalic tentacles slightly flattened; median cephalic tentacle situated at level of eyes. Occipital organ consisting of 4 pairs of oblong, slender nuchal processes, the outer and inner process of each group slightly shorter than the others. Anterior segments fused. Posterior tentacular cirri about twice as long as the anterior ventral cirri. Notopodium rudimentary. Dorsal cirri of body segments large, bean-shaped, completely covering the dorsal side.

Dorsal side of body white, with a blue sheen. Number of segments 116. Length 43 mm, width including the parapodia 3.5 mm.

Description after Imajima and Hartman (1964); not represented in our collection.

Distribution. Coasts of Japan — Sagami Bay, depth 73 m (Izuka, 1912).

17. Genus **ETEONE** Savigny, 1820, sensu lato

(incl. Mysta Malmgren, 1865; Eteonella McIntosh, 1874; Hypereteone Bergström, 1914).

Cephalic lobe with 4 small frontal tentacles at the anterior end, directed laterally; at its posterior end is a small, rounded, not always distinct nuchal papilla. One pair of eyes, sometimes with additional small eye spots (difficult to distinguish after fixation). Proboscis smooth in distal part, sometimes wrinkled, tuberculate and with large, soft papillae all around (subgenus Eteone s.str.) or with 2 distinct lateral rows of large papillae, resembling "lateral teats"; rest of dorsal part of proboscis covered with numerous small spines and denticles (subgenus Mysta). Outer opening of proboscis with rounded or threadlike oval papillae. Two pairs of spindle-shaped tentacular cirri on the 1st segment. Second segment without dorsal cirrus, but with a ventral cirrus and podial lobe. Setae absent on 1st segment. Second segment usually with acicula and setae. Formula of anterior segments: $\frac{1}{1} + S\frac{O}{N}$.

173 Parapodia uniramous, podial lobe with two short lips. Dorsal cirri small, not covering the dorsal side. Setae segmented.

The species differ mainly in the form of the dorsal cirri and in coloration; the dorsal cirri vary greatly in form in some species. The form of the anal cirri and details of the structure of the pharynx are important for the determination of species.

Over 30 species have been described, but the systematic position of many is not quite clear.

Type species: Nereis flava Fabricius, 1780.

Remarks. Bergström (1914: 209) proposed the new genus Hypereteone for Eteone lactea Claparède, 1868, because setae and acicula are absent on the 2nd segment in this species. This was not accepted by later authors. As in the genus Phyllodoce (p. 123), the presence or absence of setae and acicula on the anterior segments is only one specific character. The lack of justification for the establishment of the genus Hypereteone was also demonstrated by Eliason (1962a), who observed that large specimens of E. lactea Claparède from the Oresund had no setae on the 2nd segment, while setae are sometimes present only on one side of the segment in small specimens; this character thus seems to be related to age to some extent.

Some authors consider Mysta Malmgren as a valid genus, but I treat it as a subgenus since its species differ from those of Eteone Savigny s. str. only in the papillae on the proboscis; the proboscis has also not been sufficiently studied in all species.

Key to species of the genus Eteone Savigny, sensu lato

1 (14). Distal part of proboscis without lateral rows of teat-shaped papillae (subgenus Eteone s. str. Savigny)
2 (3). Podial lobe absent on 2nd segment . . . . 6. **E. (s. str.) lactea** Claparède
3 (2). Podial lobe present on 2nd segment.
4 (7). Dorsal cirri asymmetrical, broad (their lower margin overhanging the cirrophore like an ear).
5 (6). Dorsal side uniformly brown or greenish brown, slightly darker laterally than in the median line . . . . 4a. **E. (s. str.) spetsbergensis spetsbergensis** Malmgren
6 (5). Dorsal side light beige with two lateral brownish violet longitudinal stripes . . . . . 4b. **E. (s. str.) spetsbergensis bistriata** (Uschakov)
7 (4). Dorsal cirri symmetrical.
8 (13). Dorsal cirri oblong-oval (less wide than long or as long as wide).
9 (10). Dorsal cirri nearly twice as long as wide; eyes absent . . . . 5. **E. (s. str.) vitiazi** Uschakov
10 (9). Dorsal cirri only slightly longer than wide; eyes present but indistinct.
11 (12). Anal cirri broadly oval . . . . . . 2. **E. (s. str.) longa** (Fabricius)

174 12 (11). Anal cirri spherical . . . . 3. **E. (s. str.) delta** Wu and Chen

13 (8). Dorsal cirri broad, kidney-shaped, wider than long . . . . 1. **E. (s. str.) flava** (Fabricius)

14 (1). Distal part of proboscis with lateral rows of large, teat-shaped papillae (subgenus Mysta Malmgren).

15 (16). Dorsal cirri broad, kidney-shaped, wider than long . . . . 7. **E. (Mysta) barbata** Malmgren

16 (15). Dorsal cirri oblong-oval or conical, longer than wide or as long as wide.

17 (18). Dorsal cirri situated on high cirrophores . . . . 10. **E. (Mysta) tchangsii** Uschakov and Wu

18 (17). Dorsal cirri situated on short, broad cirrophores.

19 (20). Dorsal cirri oblong-oval. Three distinct longitudinal dark stripes on the dorsal side . . . . 8. **E. (Mysta) ornata** Grube

20 (19). Dorsal cirri conical. Dorsal side of body with punctate pigmentation, forming irregular transverse rows . . . . 9. **E. (Mysta) maculata** (Treadwell)

Subgenus ETEONE Savigny, 1829, sensu stricto

Proboscis smooth or distinctly tuberculate all around; distinct lateral rows of large teat-shaped papillae in the distal part absent.

1. **Eteone (s. str.) flava** (Fabricius, 1780) (Plate XV, Figures 4–7)

Malmgren, 1865 : 102–103, pl. XV, figs. 35–36 (E. flava and depressa); 1867 : 28, pl. II, figs. 14 (E. sarsi) and 29, pl. II, fig. 13 (E. lentigera); Théel, 1879 : 32, pl. II, fig. 20 (E. depressa); Bergström, 1914 : 196–199, textfig. 74 (synonymy); Deryugin, 1915 : 322; Ditlevsen, 1917 : 65, pl. V, figs. 2, 15, 16; Eliason, 1920 : 27; Fauvel, 1923 : 173–174, fig. 62, e–f; Augener, 1928 : 709–710 (synonymy); Annenkova, 1932a : 168; Zaks, 1933 : 127; Annenkova, 1937 : 158; 1938 : 145; Zatsepin, 1948 : 113, pl. XXIX, fig. 12, b, c, e; Ushakov, 1948a : 27; 1950 : 171; Wesenberg-Lund, 1950a : 11, map 15, pl. II, fig. 7, c; 1951 : 30; 1953 : 33, map 5; Annenkova, 1952 : 121; Grainger, 1954 : 511; Pettibone, 1954 : 235, fig. 27, g (synonymy); Ushakov, 1955a : 101, fig. 8, B; Berkeley and Berkeley, 1956 : 235; Khlebovich, 1961 : 163; Pettibone, 1963 : 74, fig. 16, f (synonymy); Levenshtein, 1966 : 8–9.

Cephalic lobe rounded anteriorly, its posterior end slightly overhanging the 1st segment; cephalic lobe wider than long. Eyes indistinct. Proboscis strongly tuberculate in distal part, sometimes with large, soft papillae all around. Tentacular cirri short, scarcely reaching to the 3rd segment; all cirri of about the same length. Podial lobe of 2nd segment with setae. Dorsal cirri in middle of body symmetrical, broader than long; they may be slightly asymmetrical on the anterior segments. Ventral cirri oval, with rounded end, about as large as the podial lobe. Shaft of setae ending in two denticles of equal size with fine spines at the articulation; distal part of setae finely serrate. Anal cirri short, broadly oval.

Coloration of body and appendages dark brown in fixed specimens. Number of segments to 300; length 40–60 mm, width including the parapodia 2– 175
4 mm (according to the literature, length to 120 mm).

Remarks. Bergström stated (1914: 106) that the proboscis of E. flava is smooth, but this is not quite correct. Malmgren's drawing, the first good one of this species, shows that the distal part of the proboscis is strongly tuberculate (Malmgren, 1865, pl. XV, fig. 35). Most specimens of E. flava examined from the northern and Far Eastern seas had a proboscis with distinct, large, tuberculate papillae all around the proboscis; similar papillae were found in E. flava from Point Barrow (Smithsonian Institution; determined by Pettibone).

Distribution. The ZIN collection has 50 specimens from the Barents, Kara, Chukchi and Bering seas and the seas of Okhotsk and Japan; depth 0–170 m. Arctic-boreal, apparently circumpolar; occurs south to the Gulf of Maine and the English Channel in the Atlantic Ocean; in the Pacific to the Sea of Japan (not in coastal waters of Japan or the Pacific coast of North America).

2. **Eteone** (s. str.) **longa** (Fabricius, 1780) (Plate XV, Figures 8–10)

Malmgren, 1867 : 26–28, pl. III, fig. 22 (E. lilljeborgi), fig. 23 (E. islandica), pl. II, figs. 12 (E. arctica), and 15 (E. leuckarti); Théel, 1879 : 32, pl. II, Figs. 23–24 (E. arctica); Webster and Benedict, 1884 : 705, pl. I, figs. 1–5 (E. cinerea); Bergström, 1914 : 192–195, textfig. 72 (synonymy); Deryugin, 1915 : 333 (E. arctica); Eliason, 1920 : 26–27; Treadwell, 1922 : 174, figs. 7–10 (E. tuberculata); Fauvel, 1923 : 172–173, fig. 62, a–d; Zenkevich, 1925 : 3; Augener, 1928 : 710; Fauvel, 1933 : 16; Zaks, 1933 : 27; Annenkova, 1934 : 322; 1937 : 158; 1938 : 145; Ushakov, 1939 : 83; Gorbunov, 1946 : 38; Zatsepin, 1948 : 113, pl. XXIX, fig. 13, b, c, e; Berkeley and Berkeley, 1948 : 41, figs. 57–58; Ushakov, 1948a : 27; 1950 : 170–171; Wesenberg-Lund, 1950a : 11, map 15, pl. II, figs. 6, 7, a–b; 1951 : 29; Annenkova, 1952 : 120; Pettibone, 1954 : 234, fig. 27, h (synonymy); Ushakov, 1955a : 101, fig. 8, A; Khlebovich, 1961 : 163–164; Pettibone, 1963 : 73–74, fig. 16, e (synonymy); Bellan, 1964 : 47; Imajima and Hartman, 1964 : 61; Ushakov and Wu Pao-ling, 1965 : 154–155; Levenshtein, 1966 : 9; Buzhinskaya, 1967 : 81.

Cephalic lobe more oblong than in E. flava, about as long as wide. Eyes small, indistinct. Proboscis distinctly wrinkled in distal part, sometimes with indistinct tubercles. Tentacular cirri short, upper and lower cirrus of about the same size. Podial lobe of 2nd segment with setae. Dorsal cirri of body segments oblong-oval, nearly symmetrical; they are broader in the anterior part of the body, narrower in the posterior part. Ventral cirri small, rounded-oval or slightly pointed. Anal cirri short, broadly oval. Setae as in E. flava.

Body and appendages light brown or yellowish beige, sometimes spotted; dorsal side with numerous small dark violet, transverse lines (dashes); according to Khlebovich (1961), mature males with a whitish tinge, mature females dark green or brown. Number of segments to 350; length about 40–50 mm, maximum length 160 mm; width 0.5–3 mm.

Remarks. Eteone japonensis McIntosh, 1901, described from
176 the Sea of Japan (superficial description, with a single drawing of a parapodium), resembles E. longa (Fabricius) and may be a synonym of this; Imajima and Hartman (1964) did not collect this species, but state that it differs from E. longa in its longer tentacular cirri.

Ecology and reproduction. This is mainly a shallow-water species, but there are some records from depths of 400–500 m. It prefers sandy-silty ground, found on mixed facies among Balanus and mussels, rhizoids of Laminaria and rhizomes of Phyllospadix. In tidal zones it burrows into sandy ground during recession of the water to a depth of 10 cm or more; it tolerates considerable freshening. It forms colonies in the Far Eastern seas with a density of to 50 specimens per m^2 (Levenshtein, 1960; Buzhinskaya, 1967), and in Danish waters to 216 specimens per m^2 (Muus, 1967). It is an active predator which attacks other polychaetes, often larger than itself (Khlebovich, 1959).

Specimens with genital products in the body cavity have been recorded from the southern Kuril Islands in March–April, and later near the northern islands, possibly due to the temperature (Khlebovich, 1961). Planktonic larvae of E. longa were found in Pos'et Bay (Sea of Japan) in May, at temperatures between 3° and 8°C (Sveshnikov, 1967). In the Murmansk region, mature specimens were found mainly from May to July. Reproduction begins in the White Sea in May at about 0°C. Mature specimens were found in April off the Atlantic coast of North America (Pettibone, 1963). Spawning in Danish coastal waters takes place in May–June. Mature specimens come to the surface, where they deposit their eggs (Meek and Storrow, 1924; Rasmussen, 1956). The development of E. longa has been studied in detail in the White Sea and in Pos'et Bay (Sveshnikov, 1961, 1967). According to Sveshnikov, larvae at the nektochete stage have 7 segments and are 450–500 μ long. On all segments, except the oral segments, are rings of cilia (nototrochs) on the dorsal and ventral side, and a telotroch on the rounded pygidium; these rings of cilia and drops of oil in the intestine enable the larva to float in the water for 2–3 days, and it then settles on the bottom (detailed description of the larva on p. 47).

Distribution. Represented in the ZIN collection by numerous specimens (over 240 stations) from northern and Far Eastern seas. A widely distributed arctic-boreal, circumpolar species; in the Atlantic Ocean it spreads to Massachusetts Bay and to the Mediterranean; in the Pacific to Hokkaido and the Yellow Sea.

3. **Eteone** (s. str.) **delta** Wu and Chen, 1963 (Plate XVI, Figures 1–6)

Wu and Chen, 1963: 30, pl. I, figs. A–E, pl. II, fig. A.

Cephalic lobe triangular. Eyes distinct. Twelve large pharyngeal papillae at distal end of proboscis; proboscis smooth, weakly wrinkled. Tentacular cirri short. Setae present on podial lobe of 2nd segment. Dorsal cirri very small, slightly oblong, a little longer than wide; they are shorter than the podial lobes on the anterior segments, larger on the posterior segments.
177 Twelve to 15 setae in a bundle. Anal cirri short, thick, rounded (spherical).

Number of segments to 109; length to 27 mm (mature specimen).

Remarks. Closely related to E. longa (Fabricius) but differs in its rounded (spherical) anal cirri and very small dorsal cirri. Not represented in the ZIN collection.

Distribution. Delta of Yangtse River, near Shanghai (salinitiy 0.12‰).

4a. **Eteone** (s. str.) **spetsbergensis spetsbergensis** Malgren, 1865

Malmgren, 1865 : 102, pl. XV, fig. 28; Théel, 1879 : 31–32, pl. II, figs. 21–22; McIntosh, 1908 : 104–106, pl. LXIX, figs. 5–6, pl. LXXVII, figs. 16–16b; Bergström, 1914 : 202–204, textfig. 77 (synonymy); Ditlevsen, 1917 : 66, pl. V, figs. 12, 14, 18; Eliason, 1920 : 27; Augener, 1928 : 708–709 (synonymy); Annenkova, 1932a : 168; Zatsepin, 1948 : 113, pl. XXIX, fig. 17, c, e; Wesenberg-Lund, 1951 : 31; Pettibone, 1954 : 235; fig. 27, f.

Cephalic lobe oblong. Proboscis distinctly tuberculate or with large, soft papillae all around. Tentacular cirri short, of the same size or the lower cirri slightly smaller than the upper. Setae of 2nd segment weakly developed or absent. Dorsal cirri broad, bean-shaped, twice as wide as long, asymmetrical, with overhanging lower margin. Ventral cirri broadly oval, slightly larger than the podial lobe. Anal cirri spindle-shaped, 3–4 times longer than wide. Denticles at articulation of rostrum of seta of different size.

Dorsal side of segments uniformly greenish brown, slightly darker laterally than in the median line (specimens in alcohol in the ZIN collection lost their coloration). Number of segments to 200; length 80–100 mm; width to 4 mm.

Distribution. The ZIN collection has 6 specimens from the Barents Sea, Novaya Zemlya, Franz-Josef Land and Spitsbergen. Recorded from the Atlantic Ocean, south to Scotland. Recorded from the coast of Alaska (Pettibone, 1954). Records from the coast of South Africa (Day, 1934 : 31) need confirmation; Day may have found E. aurantiaca Schmarda. Subspecies E. spetsbergensis bistriata Uschakov (see below): west coast of Canada, E. spetsbergensis pacifica Hartman, 1936 (= E. maculata Treadwell, 1922).

4b. **Eteone** (s. str.) **spetsbergensis bistriata** Uschakov, 1953
(Plate XVII, Figures 1–5)

Ushakov, 1953 : 208–209, fig. 2; 1955a : 104–105, fig. A–C (E. (Mysta) bistriata); Levenshtein, 1966 : 9 (E. (Mysta) bistriata).

The subspecies differs from the typical form mainly in its coloration. Proboscis with soft papillae, which form numerous longitudinal rows. Setae on 2nd segment weakly developed, sometimes absent. Dorsal cirri in middle of body segments broadly oval, kidney-shaped, asymmetrical; dorsal cirri
178 of posterior segments more elongate than those of the middle segments.
Ventral cirri large, rounded-oval, as long as the podial lobe. Anal cirri elongate, 3–4 times longer than broad. Shaft of setae with 2 denticles of different size at the articulation, the large denticle with small spines at the base.

A large brown-violet spot on the dorsal side, at the base of the parapodia. Spots fused and forming 2 distinct, dark longitudinal bands at the sides; median line of dorsum light. Three small, less distinct spots on the ventral side of each segment, the spots in the median line forming a continuous longitudinal stripe, the lateral spots forming an interrupted stripe. The pigmentation of the dorsal side is well preserved in specimens kept in alcohol, but the pigmentation of the ventral side is not retained in all specimens.

Dorsal cirri not pigmented. This coloration is typical for all specimens from Far Eastern seas — only one specimen (from the east coast of Southern Sakhalin, depth 187 m) is uniformly dark on the dorsal side (var. fuscodorsata Uschakov, 1953). E. spetsbergensis pacifica Hartman, 1936, recorded from the west coast of Canada, is characterized by its irregular spotted coloration (Berkeley and Berkeley, 1948 : 42).

Remarks. Zaks (1933) recorded E. aurantiaca Schmarda, 1861 from the Sea of Japan; it was previously known only from the southern hemisphere; this species closely resembles E. spetsbergensis Malmgren in the form of the dorsal cirri, and Zaks probably had an aberrant form of E. spetsbergensis. Hartman (1959 : 154), following Quatrefages (1865 : 152), placed E. aurantiaca in the genus Lugia Quatrefages, 1865; however, this seems unjustified because there are 2 pairs of tentacular cirri on the 1st segment, which is characteristic for the genus Eteone, while Lugia has only one pair (Fauvel, 1923 : 178); Hartman later (1965a : 17) retracted this and left aurantiaca in the genus Eteone.

Distribution. Seas of Japan and Okhotsk, Bering and Chukchi seas; depth 5—200 m (28 specimens).

5. **Eteone (s. str.) vitiazi** Uschakov, n.sp. (Plate XVIII, Figures 8—10)

Cephalic lobe oblong, slightly longer than wide. Frontal cephalic tentacles large. Eyes not recognizable. Border between cephalic lobe and 1st segment indistinct. Proboscis of our specimen retracted; the proboscis is light along the 8 anterior segments, darker laterally along the next 5 segments (the lateral papillae are apparently visible, which is characteristic for Mysta; if this is correct, this species may have to be transferred to the subgenus Mysta). Tentacular cirri of 1st segment of different length: dorsal cirri narrower and shorter, ventral cirri much larger and longer. Podial lobe of 2nd segment with setae. Dorsal cirri elongate, twice as long as broad; ventral cirri shorter, rounded. Podial lobe large, distinctly projecting outward, almost as long as the body is wide from about the 25th segment. 179 Ten to 12 setae in a bundle. Setae distinctly heterogomph, distal part finely serrate.

Fragment of anterior part of body with 33 segments: coloration light beige without pigmentation; length 5 mm, width including the parapodia but without setae 0.6 mm.

Type deposited at ZIN AN SSSR, No. 1/16326.

Remarks. E. vitiazi differs from other species in its relatively large frontal cephalic tentacles, very long podial lobes, elongate dorsal cirri and the absence of eyes.

Distribution. East of Honshu — 38°02' N and 146°33' E, depth 5475 m, silt mixed with pumice ("Vityaz," station 3575, 7 May 1957, one specimen).

6. **Eteone (s. str.) lactea** Claparède, 1868 (Plate XVI, Figures 7—9)

Bergström, 1914 : 209—211, fig. 81 (Hypereteone); Fauvel, 1923 : 175—176, fig. 63, a—d (synonymy); Pettibone, 1963 : 70—71, fig. 16, a—c (synonymy).

Cephalic lobe oblong, anterior margin rounded. Eyes small, black, indistinct (deeply embedded). Two small longitudinal grooves at the sides (sense organs?) on the posterior part of the cephalic lobe. Proboscis retracted in our specimens (smooth according to the literature). Upper tentacular cirri distinctly shorter than lower cirri. Podial lobe absent on 2nd segment. Dorsal cirri on middle segments irregularly kidney-shaped, broader than long; cirrophore entering into the dorsal cirrus. Ventral cirrus slightly larger than podial lobe. Anal cirri long and pointed. Denticles at articulation of setae with small spines (smooth according to Fauvel).

Coloration of body and appendages light beige, with fine punctate pigmentation in some places. Number of segments, according to the literature, to 400; length to 230 mm.

Distribution. The ZIN collection contains 2 specimens, one from the Oresund and one from the Atlantic coast of North America (Woods Hole). It occurs in the North Atlantic from the Gulf of St. Lawrence to Florida, and also on the European coast, western Baltic Sea, North Sea and Mediterranean; depth 0–200 m.

Subgenus MYSTA Malmgren, 1865

Proboscis with two lateral rows of teat-shaped papillae; rest of surface of proboscis covered with small spines.

7. **Eteone (Mysta) barbata** (Malmgren, 1865) (Plate XVII, Figures 6–10)

Malmgren, 1865: 101, pl. XV, fig. 34 (Mysta); 1867: 26, pl. III, fig. 20
(Mysta); Théel, 1879: 34 (Mysta); Wiren, 1883: 400 (Mysta); McIntosh,
1908: 108–109, pl. LVIII, fig. 10, pl. XLIX, fig. 10, pl. LXXVIII, fig. 19
(Mysta); Southern, 1914: 75 (Mysta); Bergström, 1914: 207–208, textfig.
79, synonymy (Mysta); Ditlevsen, 1917: 66, pl. 5, figs. 12, 17, 19 (Eteone
180 striata); Eliason, 1920: 28 (Mysta); Fauvel, 1923: 176; Augener, 1928:
711 (Mysta); Annenkova, 1937: 159; 1938: 146; Berkeley and Berkeley,
1942: 190; Zatsepin, 1948: 113, pl. XXIX, fig. 14, b, c, e, k (Mysta); Ushakov,
1948a: 27 (Mysta); 1950: 171; Wesenberg-lund, 1951: 31; Annenkova, 1952:
121; Pettibone, 1954: 233–234, fig. 27 (synonymy); Ushakov, 1955a: 102,
fig. 9, D–F; Levenshtein, 1966: 9.

Cephalic lobe broad and short, slightly wider than long. Eyes usually indistinct. Anterior part of proboscis with 2 lateral longitudinal rows of large papillae ("lateral teats"), 30–50 on each side; other parts of proboscis densely covered with small papillae of varying form, coarsely granulate or with needlelike spines. Tentacular cirri cylindrical, upper cirri nearly twice as long as lower; upper cirri extending to the 5th or 6th segment. Podial lobe of 2nd segment with setae. Dorsal cirri broad, rounded, symmetrical; cirri wider than long. Ventral cirri broadly oval, slightly larger than the podial lobe. Anal cirri elongate, 3 times as long as wide. Rostrum of shaft of setae with 2 slightly curved denticles covered with small spines at the articulation; distal part of setae elongate, with fine serration at the margin.

Specimens from the coast of Sweden and the White Sea kept in alcohol were light beige with 3 darker longitudinal stripes on the dorsal side; specimens from the Chukchi Sea and Far Eastern seas were uniformly dark greenish brown. Number of segments to 175; length to 120 mm, width including the parapodia to 7 mm.

Remarks. Plate XVII, Figure 8 shows a parapodium with the shortest and broadest dorsal cirrus; the dorsal cirri vary in form, but they are always wider than long. The elongate dorsal tentacular cirri are characteristic for E. (Mysta) barbata; they are always longer than the ventral cirri, and this distinguishes this species from E. (E.) flava, which has similar dorsal cirri.

There are variations in the armament of the proboscis, particularly of the small papillae on the dorsal side of the proboscis. Thus, one specimen from the Oresund (near the type locality) had rounded, very small (only 2μ) papillae and larger (over 8μ) triangular papillae with granulate, slightly spiny surface on the dorsal side of the proboscis between the large lateral papillae, but the smaller papillae were more numerous than the larger papillae. A specimen from the White Sea had papillae of uniform size (about 8μ), all of them with distinct, needlelike spines on the rounded surface (Plate XVII, Figure 10_{II}). Similar papillae with sharp spines were present in a specimen from the Sea of Okhotsk (10_{III}). A specimen from Bering Strait and Aniva Bay (Sakhalin) had papillae of similar size (8–12μ), but their surface was coarsely granulate and without spines (10_{IV} and 10_{V}). Very long, large papillae (to 40μ) with granulate surface were present in a specimen from the northern Kuril Islands (10_{VI}) – it was very large (120 mm). The very large size of the papillae may be related to the size of the animal, 181 but the number of spines on the papillae is usually not correlated to the size of the specimen, so that these variations are apparently not connected with age. There are apparently different populations in Soviet seas, but the small amount of material does not permit a precise description. In specimens from the White Sea and the Sea of Okhotsk examined, the papillae on the proboscis closely resemble in the form of the spines papillae of Mysta papillifera Théel from Novaya Zemlya (Théel, 1879: 33–34, pl. II, figs. 25–28). It is difficult at present to determine the status of species or subspecies of Mysta papillifera Théel; the small number of large lateral papillae indicated (only 7) is not confirmed in our material; this may be due to the fact that the proboscis of the specimens from Novaya Zemlya was not completely everted (see Bergström, 1914: 208). Fauvel (1923: 176) determined M. papillifera Théel with a question mark as E. (Mysta) picta Quatr., which we consider wrong as their dorsal cirri are quite different, and moreover, E. (Mysta) picta has not been recorded north of the English Channel.

In the elongate dorsal tentacular cirri, the form of the parapodial cirri, and coloration, E. (Mysta) barbata Mgrn. partly resembles E. trilineata Webster and Benedict, 1887 from the Gulf of St. Lawrence to Massachusetts (Pettibone, 1963).

Distribution. The ZIN collection contains 40 specimens from the Barents Sea, White Sea, East Siberian coast, Chukchi Sea, Bering Sea and the seas of Japan and Okhotsk; depth 10–418 m; it is found mainly at depths below 50 m. An arctic-boreal species, which occurs in the Atlantic to the North Sea and Irish coast, and was recorded in the Pacific only on the Asiatic coast, to the Sea of Japan.

8. **Eteone (Mysta) ornata** Grube, 1877 (Plate XVIII, Figures 1–4)

Grube, 1877 : 106; Izuka, 1912 : 201; Annenkova, 1937 : 159, 1938 : 146; Ushakov, 1955a : 105, fig. 10, A–C; Imajima and Hartman, 1964 : 65–66 (Mysta); (nec Fauvel, 1932 : 73–74; 1933 : 17–18; 1953 : 128, fig. 65, a–d; nec Day, 1967 : 140, fig. 5, 1, f–i).

Cephalic lobe broad, almost triangular. Eyes barely distinguishable in fixed specimens. Proboscis with 2 lateral longitudinal rows of papillae (according to Annenkova, who dissected the pharynx, the proboscis is not preserved in collections). Upper tentacular cirri reaching to the 5th segment, lower cirri slightly shorter. Podial lobe of 2nd segment with setae. Dorsal cirri oblong-oval, nearly symmetrical; they are shorter in the anterior part of the body, longer in the posterior part. Ventral cirri elongate, slightly longer than the podial lobe. Anal cirri large, about twice as long as broad. Setae with 2 denticles of about the same size at the articulation; small spines at base of denticles.

Coloration characteristic: body and all cirri pale yellowish beige; three distinct longitudinal dark brownish violet stripes on the dorsal side, two
182 lateral stripes at the base of the parapodia; there are also three dark longitudinal stripes on the ventral side, but they are less distinct. About 150 segments. Length about 35 mm, width 1.5–2 mm.

Remarks. The synonymy of this species is very confused. E. (Mysta) ornata Grube (Fauvel, 1932, 1933, 1953), recorded by Fauvel from the coast of India and the Yellow Sea, is probably identical with the new species E. (Mysta) tchangsii Uschakov and Wu (p. 173). E. ornata Grube from the coast of Mozambique, mentioned by Day (1957, 1967), is apparently an entirely different species according to the description and the drawings. We compared it with specimens of E. ornata from the type locality. The distinctive characters of Day's specimens from Africa are the very short and broad dorsal cirri, the absence of setae on the 2nd segment, and the structure of the proboscis, which has 4 longitudinal rows of papillae in the basal part. Grube's description was unfortunately very short and without drawings. Our specimen is the second record of E. ornata.

Distribution. The ZIN collection contains a specimen from Peter the Great Bay, depth 18–20 m; Grube did not indicate the exact locality, just stating "Northern Sea of Japan."

9. **Eteone (Mysta) maculata** (Treadwell, 1920) (Plate XVIII, Figures 5–7)

Treadwell, 1920 : 593–594, figs. 1–4 (Mysta) (nec Oersted, 1843 : 29 (species incertae sedis); nec Treadwell, 1922 : 174, = E. spetsbergensis pacifica Hartman, 1936).

Cephalic lobe broad, rounded anteriorly. Eyes large, black. Proboscis retracted in our specimens, not examined. First peristomal segment with tentacular cirri, much larger than the other segments. Second segment with a podial lobe bearing setae. Dorsal cirri very small on several following segments. They are situated on broad cirrophores in the middle of the body, symmetrical or slightly asymmetrical, as wide as long or slightly shorter than wide. Podial lobes conical, very long, almost as long as the dorsal cirrus. Ventral cirri spoon-shaped. Rostrum of setae with 2 denticles of different size at the articulation; distal part with fine serration.

Dorsal side of segments with punctate pigmentation in irregular transverse rows; ventral side light; dorsal cirri in middle of body with small spots in the middle. More than 100 segments (specimens incomplete). Length to 30 mm (to 60 mm according to Treadwell), width to 3 mm.

Remarks. One specimen in the ZIN collection is from the Gulf of Tonkin, and agrees well with the description of Treadwell (1920), particularly in the presence of 2 large eyes, the type of pigmentation, the form of the parapodia with a long podial lobe and spoon-shaped ventral cirri, and details of the structure of the setae. The second specimen from the littoral of Hainan is less typical, the cephalic lobe is longer, and the pigmentation very weak.

Fauvel (1932) considers E. (*Mysta*) *maculata* Treadwell as a synonym
183 of E. (*Mysta*) *ornata* Grube, but this is probably not correct; three dark stripes on the dorsal side are characteristic for E. (*Mysta*) *ornata* (p. 172), and there are apparently two different species, E. (M.) *maculata* Treadwell, 1920 and E. (M.) *ornata* Grube, 1877.

Distribution. Philippines, depth 44 m (Treadwell, 1920); Gulf of Tonkin and Hainan, depth 0–93 m (ZIN AN SSSR).

10. **Eteone (Mysta) tchangsii** Uschakov and Wu, 1959 (Plate XIX, Figures 1–6)

Fauvel, 1933: 17–18 (*Eteone* (*Mysta*) *ornata*); Ushakov and Wu Pao-ling, 1959: 27–28, pl. II, D–G; Kao, 1959: 143, pl. VI, fig. 3, a–f (*Eteone* sp.); Ushakov and Wu Pao-ling, 1965: 155–156, fig. 2, A–D.

Cephalic lobe slightly conical, broad. Cephalic tentacles short. Eyes not recognizable. There is a small occipital papilla. Tentacular cirri relatively short, upper cirri slightly longer than the lower; they reach to the 4th setose segment. Setae present on 2nd segment. Proboscis very large (to 15 mm long), with lateral rows of large, soft papillae and indistinct transverse folds, densely covered on the dorsal side with small dark tubercles with chitinized spines. Anterior part of proboscis markedly widened, with a large teatlike dorsal process; opening surrounded in its upper part by soft, slender, finger-shaped processes (lobular border). Dorsal cirri situated on large oblong cirrophores, they are relatively small, oval, as long as or slightly shorter than the cirrophore. Ventral cirri small and blunt. About 30 setae in a bundle. Rostrum of seta with 2 denticles of different size, with small spines at the articulation.

Coloration of body and dorsal cirri yellowish brown; dorsal side distinctly darker than ventral side, with a blue sheen, iridescent in some specimens. Numerous irregularly scattered dark spots (with a violet tinge) across each segment on the dorsal side which extend partly to the cirrophores of the dorsal cirri; in specimens from Hainan, the spots form two distinct transverse stripes on each segment; pigmentation of dorsal cirri most intense at the apical margin. Number of segments to 300; length to 160 mm, width 8 mm.

Mature females with large, reddish eggs in the parapodia were recorded from the Yellow Sea on 11 November and 23 December 1950.

Remarks. This species was recorded by Fauvel (1933) from the Yellow Sea as E.(Mysta) ornata Grube. I compared our specimen of E. (Mysta) tchangsii with Fauvel's E.(M.) ornata from the Yellow Sea in the Muséum National d'Histoire Naturelle, and did not find any important differences. As already stated, E. ornata Grube is a valid species and differs distinctly from E.(M.) tchangsii in its coloration (3 longitudinal dark stripes on the dorsal side) and in the dorsal cirri (situated on short cirrophores); Fauvel stated that his E.(M.) ornata from the Yellow Sea (i.e. E.(M.) tchangsii) resembles E.(M.) siphonodonta (Delle Chiaje) from the Mediterranean in the form of the parapodia and size, and differs from it only in coloration and details of the structure of the proboscis.

184 Distribution. The ZIN collection contains 8 specimens from the Yellow Sea (Tsingtao) and the South China Sea (Hainan), from the tidal zone of sandy beaches. Fauvel apparently obtained his specimens from the coast of India (1953).

Subfamily Lopadorhynchinae Claparède, 1870

Cephalic lobe small, partly or completely fused with the 1st segment, sometimes also with the 2nd segment. Four cephalic tentacles. Two or three tentacular cirri. Two or three anterior body segments sometimes with very large parapodia, with simple hooklike setae (genus Lopadorhynchus). Pygidium with rudimentary anal appendages, or without appendages. Body short, consisting of relatively few segments (at most 35). Pelagic forms.

This subfamily contains 4 genera: Lopadorhynchus Grube, Pelagobia Greeff, Maupasia Viguier and Pedinosoma Reibisch, possibly of different origin (see p. 68).

K. Støp-Bowitz (1948) also placed the genus Nans Chamberlin, 1919 in this subfamily, which is entirely without segmented setae and has only acicular and simple hooklike setae. The systematic position of this genus is not clear. Chamberlin thinks that it forms the subfamily Nantinae. We think that the genus Nans is more closely related to the family Typhloscolecidae than to the family Phyllodocidae.

18. Genus **LOPADORHYNCHUS** Grube, 1855

(nom. corr. Kleinberg, 1886)

(Lopadorhynchus Grube, 1885; Hydrophanes Claparède, 1870; Mastigethus Chamberlin, 1919)

Cephalic lobe blunt anteriorly, very short, markedly wider than long. Cephalic lobe fused with the first 2 segments. Dorsal pair of cephalic tentacles situated at the sides of the anterior margin of the cephalic lobe; ventral pair situated close to the mouth. One pair of eyes present only in juveniles, becoming reduced later. Pharynx short, smooth or with lateral, soft, finger-shaped papillae with 3 (rarely 4) large glands. Three pairs of tentacular cirri, the 3rd pair situated on the ventral side; it is rudimentary and has the form of a small round papilla; setae and acicula at base of tentacular cirri absent. Formula of anterior segments: $1 + O\frac{1}{1} + C\frac{N}{N}$. Two, sometimes 3, anterior setose segments markedly larger than the others, with markedly modified parapodia with large, simple, curved setae. Normal body segments with a conical podial lobe, covered anteriorly by a large, rounded lip. Setae forming a broad fan. Their distal part has the form of a broad sword, with denticles on one side. Dorsal and ventral cirri shorter than the podial lobe. Anal lobe without appendages. Small number of segments. Pelagic forms.

Type species: Lopadorhynchus brevis Grube, 1855.

Some authors distinguish two subgenera, Lopadorhynchus Grube s. str. and Prolopadorhynchus Bergström because of the presence or 185 absence of a ventral cirrus on the modified anterior segments, but this character is of uncertain value (Tebble, 1960; Kim In-bae, 1967). The genus contains 7 species. A key to all species of Lopadorhynchus was given by Dales (1957). Four species have been recorded from the Northwest Pacific: L. appendiculatus Southern, L. uncinatus Fauvel, L. krohnii (Clap.), and L. brevis Grube.

Key to species of the genus Lopadorhynchus Grube

1 (2). First 3 segments with modified parapodia . . . . 2. **L. brevis** Grube
2 (1). First 2 segments with modified parapodia.
3 (4). Parapodia of two anterior segments with a fringe in the form of a comb or a collar . . . . 4. **L. uncinatus** Fauvel
4 (3). Parapodia on two anterior segments without a fringe.
5 (6). Ventral cirri with very long, slender end. Simple setae absent from the 4th segment onward . . . . 1. **L. appendiculatus** Southern
6 (5). Ventral cirri tapering. One or 2 simple setae on all body segments near the ventral cirrus . . . . 3. **L. krohnii** (Claparède)

1. **Lopadorhynchus appendiculatus** Southern, 1909 (Plate XX, Figures 1–5)

Southern, 1909 : 7–9, pls. II–III, figs. 12–20; Bergström, 1914 : 179, textfig. 66 (Prolopadorhynchus); Fauvel, 1923 : 187–188, fig. 69, a–i; Wesenberg-Lund, 1939 : 17–19, figs. 13–14; Støp-Bowitz, 1948 : 20–21; Ushakov, 1957 : 271–272, fig. 2, a–e, map 1; Kim In-bae, 1967 : 228–230, figs. 4, d, 5, a, b, c.

Upper cephalic tentacles markedly larger than the lower. Tentacular cirri (not including the 3rd rudimentary pair on the ventral side) larger than cephalic tentacles. Two first setose segments larger than the others, with thick, blunt podial processes which have an undulate fringe (folds) at the distal end; below it are situated large, simple, hooklike setae with strongly curved end in a semicircle; the setae are partly yellowish brown; there are 6–7 on each parapodium. Ventral cirri on first two anterior modified parapodia weakly developed and forming a separate part of the fringe. Ventral cirri on all following parapodia with very long, threadlike end, which distinguishes this species from the others. Parapodia of normal segments with a conical podial lobe with an aciculum, a broad anterior semicircular lip and with a bundle of complex setae arranged in a fan. There are 1 or 2 simple, light setae in the lower part of the bundle on the 3rd pair of parapodia; simple setae absent on other body segments. Denticle at the articulation of setae asymmetrical; distal part very broad, like the blade of a knife, slender, transparent, with small denticles on one side. Anal lobe semicircular; anal cirri absent.

Coloration yellowish. Number of seta-bearing segments 24. Length 10 mm, width including the parapodia and setae 2.5 mm.

186 The specimen examined was a mature female, with eggs in the parapodia (13 September 1953).

Distribution. The ZIN collection has one specimen from the Northwest Pacific, Kuril Islands, 43°20' N and 155°47' E, depth 0–50 m. According to the literature, it occurs in the Atlantic Ocean near Ireland, the Azores and Canary Islands, also in the Mediterranean; a rare species.

2. **Lopadorhynchus brevis** Grube, 1855

Grube, 1855 : 100, pl. 3, figs. 13, 15, 16; Reibisch, 1895 : 38, pl. 3, figs. 10–15 (nationalis); Chamberlin, 1919a : 114–119, pl. 17, figs. 1–7 (parvum and nans); Fauvel, 1923 : 184, fig. 69, k; Monro, 1930 : 78; 1937 : 266–267; 1939 : 347; Wesenberg-Lund, 1939 : 12–15, figs. 8–10, map 7; Støp-Bowitz, 1948 : 18; Dales, 1957 : 104–105, figs. 7–8; Berkeley and Berkeley, 1958 : 401; Tebble, 1960 : 200–201, 259–261, figs. 52; 1962 : 416–417; Berkeley and Berkeley, 1964 : 122; Rullier, 1965c : 867–868; Kim In-bae, 1967 : 219–221, figs. 1–3 (synonymy).

Upper and lower cephalic tentacles of about the same length. First three pairs of parapodia larger than the others, only with large, simple, slightly curved setae (7–10 on a parapodium). Ventral cirri recognizable only from the 3rd setose segments; ventral cirrus at first awl-shaped-conical, then oblong-pear-shaped (its form changes on the 12th–14th segments). Parapodia with complex (segmented) setae from the 4th segment and usually also with 1 or 2 simple setae. Number of segments to 35; length to 35 mm, width to 7 mm.

Distribution. The ZIN collection has 2 specimens from the Mediterranean and 14 specimens collected by the Soviet Antarctic expedition ("Ob") in the southern parts of the Pacific and in the tropical zone of the Indian Ocean (Tebble, 1968). According to the literature, it is restricted to the tropical and subtropical zones of the Atlantic, Indian and Pacific oceans. Recorded from the coasts of Japan and California. It makes daily vertical migrations in California and is found on the surface only at night (Dales, 1957).

3. Lopadorhynchus krohnii (Claparède, 1870)

Claparède, 1870 : 100–102, pl. XI, fig. 2 (Hydrophanes); Reibisch, 1895 : 35, 37–38, pl. 4, fig. 4 (viguieri); Bergström, 1914 : 180–182, fig. 68; Wesenberg-Lund, 1939 : 15–16, fig. 11, map 8; Dales, 1957 : 105–106, figs. 9, 10; Tebble, 1960 : 202, 259–261, fig. 52; 1962 : 418–419, fig. 21; Berkeley and Berkeley, 1964 : 122; Kim In-bae, 1967 : 226–228, fig. 4, c (synonymy).

Dorsal pair of cephalic tentacles slightly larger than the ventral pair. First two pairs of parapodia distinctly thicker than the others and only with large, curved, simple setae which are not surrounded by a fringe (collar) as in L. *uncinatus* Fauvel. Ventral cirri on first two segments fused with the posterior podial lobe and distinct only from the 3rd segment onward. Parapodia of normal body segments with numerous segmented and 1 or 2 hooklike simple setae near the ventral cirrus. Number of segments to 20; length to 9 mm.

187 *Distribution.* ZIN collection: 19 specimens from the tropical zone of the Indian Ocean and southern parts of the Pacific (collected by the "Ob" expedition, 1956–1958) (Tebble, 1968). Recorded from the tropical and subtropical regions of the Atlantic, Indian and Pacific oceans, also near the coast of Japan and California.

4. **Lopadorhynchus uncinatus** Fauvel, 1915

Fauvel, 1915 : 3, fig. 2; 1923 : 184–185, fig. 67, a–g; Wesenberg-Lund, 1939 : 10–12, figs. 6–7, map 6; Treadwell, 1943 : 32–33, pl. 1, figs. 7–10 (*varius*); Støp-Bowitz, 1948 : 17–18, fig. 11; Dales, 1957 : 101–104, figs. 1–6; Berkeley and Berkeley, 1958 : 400–401; 1960 : 788; Tebble, 1960 : 259–261, fig. 52; 1962 : 417; Berkeley and Berkeley, 1964 : 122; Kim In-bae, 1967 : 225, fig. 4, a, b.

Dorsal pair of cephalic tentacles longer than the ventral pair. First two pairs of parapodia much larger than the others; they are without ventral cirri, with 4–7 very large, curved, simple setae which are surrounded by a distinct fringe like a comb or a collar. Numerous segmented setae on the other segments, sometimes also 1 or 2 simple setae. Number of segments to 32; length to 25 mm, width to 7 mm.

Distribution. ZIN collection: one specimen from the tropical zone of the Indian Ocean ("Ob" expedition, 1957). Mainly in tropical and subtropical zones of the Atlantic, Indian and Pacific oceans, also from the coast of Japan.

19. Genus **PELAGOBIA** Greeff, 1879

Cephalic lobe oblong, rounded anteriorly, indistinctly separated from the 1st segment. Eyes absent or present and with a lens. Pharynx with two chitinous styletlike hooks and numerous glands. Two pairs of long tentacular cirri on 1st segment; a bundle of longe setae at base of tentacular cirri. Dorsal cirri absent on 2nd segment. Formula of anterior segments: $S\frac{1}{1} + S\frac{O}{N} + S\frac{N}{N}$. Parapodia uniramous, long. Dorsal and ventral cirri elongate, cylindrical, finger-shaped, much longer than the podial process. All setae segmented, with denticulate distal part. Anal lobe with 2 anal cirri. At most 25 segments. Small pelagic species; body semitransparent.

Type species: *Pelagobia longicirrata* Greeff, 1879.

The genus contains two species. P. *erinensis* Nolte, 1938 has 4 setose segments in the postlarval stage.

A detailed description of the pharynx of *Pelagobia longicirrata*, with a drawing of the small hooks, was given by Friedrich (1949). The hooks in the pharynx of *Pelagobia* resemble those of *Phalacrophorus* (p. 183).

Key to species of the genus Pelagobia Greeff

1 (2). Eyes present. Distal end of shaft of setae smooth or with very small (microscopic) spines . . . . 1. **P. longicirrata** Greeff

188 2 (1). Eyes absent. Distal end of shaft of setae with large spines . . . . * **P. serrata** Southern 1909

Southern, 1909 : 3, pl. I, figs. 2–3.
Coast of Ireland, Azores,
Mediterranean (Monaco)

1. **Pelagobia longicirrata** Greeff, 1879 (Plate XXI, Figures 1–4)

Greeff, 1879 : 247, pl. XIV, figs. 23–25; Reibisch, 1895 : 21, pl. II, figs. 1–9 (longecirrata); Gravier, 1911 : 62–65, pl. II, figs. 22–25 (P. viguieri); Ehlers, 1913 : 460–462; Bergström, 1914 : 186–187, textfig. 70; Chamberlin, 1919a : 122–124 (P. viguieri); Benham, 1921 : 57, pl. 7, figs. 59–60 (P. viguieri); Fauvel, 1923 : 192, fig. 72, a–e; Benham, 1927 : 78 (P. viguieri); Augener, 1929 : 291–294; Okuda, 1937a : 75–76, fig. 1; Yashnov, 1940 : 58; Treadwell, 1943 : 33 (P. viguieri); Støp-Bowitz, 1948 : 21; 1949 : 4–5; Wesenberg-Lund, 1950b : 37–38, map 9; Ushakov, 1952 : 103–104, fig. 1 (P. viguieri); 1955a : 105–106, fig. 11, A–C (P. viguieri); 1957a : 268, map 1; Dales, 1957 : 107–108, figs. 11–13; Tebble, 1960 : 202–204, 237–242, figs. 37–44, pls. 18, 19; Berkeley and Berkeley, 1960 : 788; Imajima, 1961 : 6; Tebble, 1962 : 419–420, fig. 22; Berkeley and Berkeley, 1964 : 123.

One pair of eyes with a distinct lens. Two large pigmented occipital organs at sides of cephalic lobe. Two pairs of long, cylindrical tentacular cirri which are as long as the 4–6 anterior setose segments; a large bundle of segmented setae at base of tentacular cirri. Parapodia with a conical process and a bundle of long, segmented setae. First pair of parapodia without dorsal cirrus; all following parapodia with long cylindrical dorsal cirri. Ventral cirri on all segments of the same form as the dorsal cirri, but slightly shorter. Dorsal and ventral cirri markedly longer than the podial lobe. All setae complex (segmented), distinctly heterogomph, with two denticles of different size at the articulation; distal part long, with a few, large denticles at one margin and a slender delicate blade, or border, at the other; distal part of shaft smooth or with very small, microscopic spines (shaft smooth in my specimens). Setae very long, distinctly projecting outward. Anal lobe with rudimentary appendages.

Body semitransparent, yellowish gray; there are bright orange-yellow spots at the sides of the segments and at the base of the podial cirri in some specimens. Number of setose segments 14–17 (maximum 25). Length 8 to 12 mm, width to 2 mm.

Distribution. ZIN collection: specimens from the Norway Sea, Polar Basin, Sea of Okhotsk, Northwest Pacific, and from various regions of the southern hemisphere (140 stations). Small concentrations have been recorded at horizons of 200–1000 m from the Kuril Islands, density one specimen per m^3 (Mileikovskii, 1969). A widely distributed, bathypelagic species.

189 20. Genus MAUPASIA Viguier, 1886

(Halyplanes Reibisch, 1893; Haliplanes Reibisch (1894) 1895; Haliplanella Treadwell, 1943)

Cephalic lobe very short, rounded anteriorly, fused with the 1st segment. Eyes absent. Pharynx short, without papillae but with large glands. Three pairs of tentacular cirri, 2 pairs on the 1st segment, 3rd pair on the 2nd segment, which is more or less clearly demarcated from the 1st segment. Near the tentacular cirri are acicula and setae. Formula of anterior segments: $S\frac{1}{1}) + S\frac{1}{N} + S\frac{N}{N}$. Third pair of tentacular cirri sometimes very long, much larger than the first two pairs. Parapodia uniramous, with dorsal and ventral cirri. Setae segmented, with elongate, slender distal part; simple setae may be present on the 1st segment. Anal lobe with rudimentary appendages. Number of segments small (usually at most 20). Small pelagic forms, 7–8 mm long.

Remarks. Species of the genus Maupasia often have at the sides of the cephalic lobe, near its posterior margin, long nuchal papillae (vibratile organs), which may be mistaken for tentacular cirri. Tebble (1962 : 421) described 4 pairs of tentacular cirri for this genus and gave the formula $\frac{1}{1} + \frac{1}{1}$; he apparently considered the elongate nuchal processes as the first pair of tentacular cirri, but his drawing shows clearly that there is only one pair of tentacular cirri on the 2nd segment. All my specimens show the formula given by Fauvel (1923).

Type species: Maupasia caeca Viguier, 1886.

The genus contains 4 species.

Key to species of the genus Maupasia Viguier

1 (2). Dorsal tentacular cirri of 2nd segment about as long as cirri on 1st segment. Dorsal podial cirri leaf-shaped, broad, with long, teat-shaped end; ventral cirri long and pointed . . . 1. **M. caeca** Viguier

2 (1). Dorsal tentacular cirri of 2nd segment much longer than tentacular cirri of 1st segment.

3 (4). Dorsal podial cirri leaf-shaped . . . . ***M. gracilis** (Reibisch)

Reibisch, 1895 : 25–26, pl. II, figs. 10–14 (Haliplanes); Southern, 1909 : 5, pl. I, fig. 6, pl. II, figs. 7–11 (Haliplanes magna); Treadwell, 1943 : 32, pl. I, figs. 4–6 (Haliplanella pacifica); Dales, 1957 : 108

Atlantic Ocean (from 10° S to 40° N) and equatorial regions of the Pacific

4 (3). Dorsal podial cirri oblong-oval.

5 (6). Setae on all segments of about the same thickness . . . . ***M. isochaeta** (Reibisch)

Reibisch, 1895 : 26–27, pl. II, fig. 14 (Haliplanes). Atlantic Ocean (Sargasso Sea) and Mediterranean

190 6 (5). Some very thick, short segmented setae on the anterior parapodia; all setae of about the same thickness on the posterior segments . . . . 2. **M. brodskyi** Uschakov

1. **Maupasia caeca** Viguier, 1886 (Plate XXI, Figures 5—8)

Viguier, 1886 : 382—385, pl. XXI, figs. 14—20; Ehlers, 1913 : 462; Fauvel, 1923 : 190—191, fig. 71, a—d; 1939 : 276—277; Wesenberg-Lund, 1939 : 19—20, map 11; Ushakov, 1957a : 268—270, fig. 1, c—e, map 1; Berkeley and Berkeley, 1958 : 401; Tebble, 1960 : 204—205, 242, fig. 44; 1962 : 421—423, figs. 23, 24; Berkeley and Berkeley, 1964 : 123.

Two large, rounded swellings (nuchal organs) at the posterior margin of the cephalic lobe on the dorsal side laterally. First segment indistinctly separated from cephalic lobe, with 2 pairs of elongate tentacular cirri with a small bundle of setae at the base. Second segment with one pair of elongate tentacular cirri, podial lobe with setae and a short ventral cirrus (distinctly shorter than on the other segments). Tentacular cirri of 2nd segment about as long as width of body. Dorsal cirrus broadly leaf-shaped, with long, pointed end; ventral cirrus very long, pointed, longer than the podial lobe. Setae numerous, long, thin, scattered; all setae of the same type, with heterogomph articulation, distal part long and thin. Body tapering posteriorly. Number of segments 15. Our specimens are mature females, with large eggs in the body cavity and in the parapodia. Body not pigmented, light beige. Length to 4 mm, width (without setae) 1.5 mm.

Distribution. The ZIN collection has 2 specimens, collected east of the Kuril Islands — 43°08' N, 156°08' E, horizon 0—600 m (23 July 1953), and 6 specimens from the Indian Ocean and the Antarctic (collected by the "Ob" expedition 1956—1958). Widely distributed, pelagic species: coast of Ireland, Bay of Biscay, Mediterranean, equatorial and southern regions of the Atlantic Ocean, coast of Indo-China, Pacific Ocean from the Bering Sea to the coast of Peru.

2. **Maupasia brodskyi** Uschakov, 1957 (Plate XXI, Figures 9, 10)

Ushakov, 1957 : 270—271, fig. 1, a—b, map 1.

Two branched occipital nuchal organs at sides of cephalic lobe. First segment fused with cephalic lobe and with 2 small, short tentacular cirri on each side, there are small setae (apparently simple) at their base. Second segment distinctly demarcated from 1st segment, with large dorsal tentacular cirri at the sides which are longer than the width of the body; ventral cirri on parapodia of 2nd segment very small. All following segments of the same form; their dorsal and ventral cirri oblong oval. Setae segmented, heterogomph, of varying thickness. There are several (2 or 3) very thick, shorter segmented setae with a small distal part in addition to slender setae
191 on the anterior segments; all setae of about the same thickness and length on the posterior segments. Number of segments 14. Body almost transparent; length about 2 mm, width 1 mm.

Type deposited at ZIN AN SSSR, No. 1/16862.

Distribution. Northwest Pacific — 34°02' N, 148°49' E, horizon 50—0 m (one specimen).

21. Genus **PEDINOSOMA** Reibisch, 1895

Cephalic lobe rounded anteriorly, very short, fused with the 1st segment. Pharynx smooth, without papillae. Two pairs of tentacular cirri on the 1st segment, setae near the cirri absent. Formula of anterior segments: $O\frac{1}{1}) + S\frac{N}{N}$. Parapodia uniramous. Dorsal cirri rounded, small, ventral cirri long and pointed. Setae segmented. Anal lobe without appendages. Very small pelagic species.

Type species: *Pedinosoma curtum* Reibisch, 1895.

This genus is monotypic.

The structure of the anterior end is not clear. According to Fauvel (1923), the cephalic lobe is fused only with the 1st segment, which bears 2 pairs of tentacular cirri; according to Bergström (1914), the cephalic lobe is fused with the first 2, reduced segments; in the former case the formula is $O\frac{1}{1}$, and in the other case $1 + O\frac{1}{(i)}$. If the first formula is correct, *Pedinosoma* is closely related to *Maupasia* and *Pelagobia*, and if the second formula is correct, it is more closely related to *Lopadorhynchus*, in which the cephalic lobe is fused with first two segments (p. 174).

1. **Pedinosoma curtum** Reibisch, 1895 (Plate XXII, Figures 4, 5)

Reibisch, 1895 : 21, 27—30, pl. II, fig. 17, pl. III, figs. 1—4; Fauvel, 1916 : 64; 1923 : 188—189, fig. 70, c—f; Berkeley and Berkeley, 1960 : 789; Tebble, 1962 : 424—425, figs. 25—26.

Cephalic lobe broad, with 2 lateral sense organs at the posterior margin in the form of small tubercles with cilia. Tentacular cirri large, pointed, longer than the width of the body. Setae near tentacular cirri absent. Parapodia with large, conical podial lobe. Dorsal cirri round or oval, flattened; ventral cirri very long, cylindrical, with pointed end. Distal part of setae very long and thin.

Length 1—3 mm; 7 or 8 setose segments.

Distribution. ZIN collection: one specimen from the Northwest Pacific — 31° N, 155° E. Very rare, a few isolated records from the Northeast Pacific, tropical and subtropical zones of the Atlantic Ocean and Mediterranean.

92 Subfamily Pontodorinae Bergström, 1914

Cephalic lobe small, fused with the first 2 segments. Two cephalic tentacles. Two pairs of tentacular cirri. All body segments with a very long podial lobe which has the form of a cirriform appendage. Dorsal and ventral cirri very small. Two anal cirri. Body short, number of segments at most 20. Pelagic forms.

The subfamily contains a single genus, Pontodora Greeff, 1879.

22. Genus PONTODORA Greeff, 1879

(Epitoka Treadwell, 1943)

Cephalic lobe with 2 very long tentacles at the anterior end. Pharynx short, barrel-shaped, muscular, with oblong papillae. Two pairs of elongate tentacular cirri, the first pair situated distinctly anterior to the second pair near the mouth; setae near the tentacular cirri absent. Formula of anterior segments (probably): $1 + 1) + S\frac{O}{N}$. Podial lobes of all body segments forming long, finger-shaped processes with a large internal seta (aciculum); dorsal and ventral cirri situated at base of podial lobe. Dorsal cirrus absent on 1st setose segment. Anal lobe with 2 very long anal cirri. Setae segmented, with thin distal part. Fewer than 20 segments; body transparent. Very small pelagic species.

Type species: Pontodora pelagica Greeff, 1879.

Monotypic genus.

Treadwell (1943) described the new genus Epitoka and placed it in the family Syllidae. The descriptions and drawings of this genus are not sufficiently exact and were made from a macerated specimen. However, according to the important characters, the specimen belongs to the genus Pontodora Greeff.

1. **Pontodora pelagica** Greeff, 1879 (Plate XX, Figures 6–8)

Greeff, 1879: 245–247, pl. XIV, figs. 19–22; Viguier, 1886: 388–392, pl. XXII, figs. 17–19; Reibisch, 1895: 17–18; Viguier, 1920: 256–259, pl. I, figs. 4–6; Fauvel, 1923: 197, fig. 73, f–k; ? Treadwell, 1943: 40 (Epitoka pelagica); Ushakov, 1957: 273–274, fig. 3, a–c, map 1; Berkeley and Berkeley, 1960: 728; 1964: 121–122.

Cephalic lobe blunt, slightly rounded anteriorly; one pair of small, reddish eyes. Cephalic tentacles and tentacular cirri of about the same form and length, the first pair of tentacular cirri situated distinctly anteriorly, nearly at the level of the cephalic tentacles. Podial lobes with a finger-shaped process which is longer than the width of the body. Dorsal and ventral cirri small, oblong-oval, flattened; there are small ciliary organs (ctenidia) at the base of the podial process. Only one pair of podial cirri on 1st setose segment; their position is not clear, ventral or dorsal, in our preparations. Setae numerous, thin, long, all of them segmented: shaft with 193 two denticles of different size at the articulation; distal part thin, with small denticles on one side. Body transparent, numerous with adipose inclusions. There are 4 orange-yellow star-shaped spots on each segment, particularly in the anterior part of the body, 2 at the base of the parapodia and 2 on the dorsal side of the segment; there are also similar small spots on the podial processes. Number of segments 17–18; length 2–5 mm, width excluding the podial processes and setae 0.2–0.5 mm.

Distribution. The ZIN collection contains 15 specimens: from the Northwest Pacific, south of the Kuril Islands and east of Honshu. Described from subtropical regions of the Atlantic Ocean (Canary Islands) and the Mediterranean; recorded from the Northwest Pacific (Berkeley and Berkeley, 1960) and from the coast of Peru (Berkeley and Berkeley, 1964).

Subfamily Iospilinae Bergström, 1914

Cephalic lobe small, fused with the 1st segment. Two cephalic tentacles (?palps). Two pairs of tentacular cirri. Two or several anterior segments with reduced parapodia. Dorsal and ventral cirri small. Anal cirri absent. Body short, number of segments at most 60. Pelagic forms.

The subfamily contains 4 genera: Phalacrophorus Greeff, 1879, Iospilus Viguier, 1886, Pariospilis Viguier, 1911, and Iospilopsis Augener, 1922. The first genus has a pharynx with 2 large chitinized hooks, a character which is absent in the Phyllodocidae, except in Pelagobia (p. 177). Our material contains only species of the genus Phalacrophorus.

23. Genus **PHALACROPHORUS** Greeff, 1879

Cephalic lobe with 2 small tentacles on the ventral side near the mouth (?palps). Eyes present or absent. Pharynx with two large lateral chitinized hooks. Two pairs of small tentacular cirri, setae absent near the first pair, and there is a small podial lobe with a bundle of setae near the second pair. Two or more anterior setose segments without podial cirri. Dorsal and ventral cirri of the parapodia of the following segments very small, shorter than the podial lobe. All setae segmented, with long, thin distal part. Borders between segments indistinct. Number of segments 30–60. Spots at base of parapodia, body transparent.

Type species: Phalacrophorus pictus Greeff, 1879.

The genus contains 2 species and 1 subspecies. Ph. niger Treadwell (1943), from the coast of Peru and equatorial regions of the Pacific Ocean, belongs to the genus Iospilus Viguier (see Dales, 1957 : 108).

Key to species of the genus Phalacrophorus Greeff

1 (4). Only the 4 anterior segments with reduced parapodia. Number of segments 20–30.

2 (3). Eyes present . . . . 1a. **Ph. pictus pictus** Greeff

194 3 (2). Eyes absent . . . . 1b. **Ph. pictus borealis** Reibisch

4 (1). Eight to 10 anterior segments with reduced parapodia. Number of segments to 60 . . . . *** Ph. uniformis** Reibisch, 1895

Reibisch, 1895 : 15–17, pl. I, figs. 10–16; Treadwell, 1943 : 34, fig. 14 (Ph. attenuatus); Tebble, 1962 : 426–428, fig. 27, a, b. Tropical and subtropical regions of the Atlantic and Pacific

1a. **Phalacrophorus pictus pictus** Greeff, 1879 (Plate XXII, Figures 1, 2)

Greef, 1879 : 249–251, pl. XIV, figs. 26–30; Viguier, 1886 : 395–402, pl. XXIII, figs. 7–18; Reibisch, 1895 : 10–12, pl. I, figs. 4–7; Ehlers, 1913 : 460; Fauvel, 1923 : 196, fig. 72, f; Augener, 1929 : 290–291; Treadwell, 1943 : 34, pl. I, figs. 11–13 (Ph. maculatus); Dales, 1957 : 109; Ushakov, 1957a : 274–275, fig. 3, d–e, map 1; Berkeley and Berkeley, 1957 : 573–574; 1964 : 123; Mileikovskii, 1961 : 1101–1102, figs. 3–4; Tebble, 1962 : 426, fig. 27, c.

One pair of dark brown eyes with small lenses. Pharynx massive, muscular, with 2 large, sharply curved chitinized hooks at the anterior end. First pair of tentacular cirri much shorter than the second pair; only second pair of tentacular cirri with setae (2 or 3). The two following segments with rudimentary parapodia with 2 or 3 setae, without dorsal and ventral cirri. Borders between segments indistinct. Podial lobes gradually increasing in size, on the middle segments having the form of large, conical processes with a bundle of very thin, long segmented setae. Dorsal and ventral cirri small, rounded, shorter than the podial lobes. Anal lobe rounded, strongly pigmented. Body semitransparent, with yellowish brown pigmented spots at the bases of the parapodia on the dorsal side. Number of segments 20–30. Length to 6 mm.

Distribution. The ZIN collection contains specimens from the Norway and Barents seas and the Northwest Pacific (6 specimens). Reported from the North Atlantic, Mediterranean, southern part of the Atlantic (Rio de Janeiro), and northern parts of the Pacific; coast of South America (Chile).

1b. **Phalacrophorus pictus borealis** Reibisch, 1895 (Plate XXII, Figure 3)

Reibisch, 1895 : 12–15, pl. I, figs. 8–9, pl. VI; Ditlevsen, 1914 : 690; Wesenburg-Lund, 1953 : 31; Ushakov, 1957 : 1662, fig. 2.

Eyes absent. Pharynx massive, with 2 slightly curved chitinized hooks. Two pairs of small tentacular cirri, with 2 or 3 setae only on the second pair. Anterior 2 body segments with reduced parapodia. Parapodia in the form of conical processes with a bundle of long, thin setae; distal part of setae long, thin. Dorsal podial cirri rounded, shorter than the podial lobes. Body semitransparent; unlike Ph. pictus pictus, without pigmented spots. Number of segments to 20. Maximum length 3 mm (our specimens were at most 2 mm long).

195 Remarks. Dales (1957) considers Ph. borealis Reibisch as a juvenile of Ph. pictus Greeff, from which borealis differs in its smaller size, the absence of eyes, and less curved pharyngeal hooks; in our opinion, it is a distinct form which inhabits cold northern waters, as is also assumed by Tebble (1962 : 466).

Distribution. Our material contains 2 specimens from the central regions of the Polar Basin (horizons 275–0 and 925–275 m). Recorded from the east coast of Greenland.

II. Family Alciopidae Ehlers, 1864*

Body relatively long and thin, slightly thicker anteriorly and tapering posteriorly; number of segments usually large.

Cephalic lobe with 2 enormous telescopic eyes with large lenses; distance between eyes smaller than their width. Eyes often red in live specimens, dark brown or black in fixed material. Axis of eyes directed anteriorly or laterally, sometimes upward or downward.

Usually 5 small cephalic tentacles, 4 at the anterior margin of the cephalic lobe, forming 2 pairs of frontal tentacles; the median single tentacle on the dorsal side of the cephalic lobe, between the eyes, is sometimes reduced to a small, rounded tubercle.

Pharynx eversible; proboscis with soft marginal papillae and often with 2 long lateral cirriform appendages (horns) at the distal end; chitinized jaws absent.

Three anterior circumoral segments with 3–5 pairs of tentacular cirri: always one pair on the 1st segment, 2 pairs sometimes on the 2nd and 3rd or only on the 3rd segment, so that the formula is: $1 + \frac{1}{\text{O or } 1} + \frac{1}{\text{O or } 1 \text{ or } N}$, the symbols as in the formula for the Phyllodocidae (p. 64) — 1 = tentacular cirrus, O = tentacular cirrus absent, N = normal podial cirrus, + = separation of segments, and — (fraction line) = dorsal and ventral podial appendages.

Juveniles sometimes with 1 or 2 small setae at the base of the tentacular cirri, which are never present in adult specimens. Several anterior body segments behind the circumoral segment have strongly reduced parapodia in some genera, with a few setae, which may also be absent. Mature females of some species often with dorsal cirri on 2 segments (4th – 6th) which are modified into large pockets, receptacula seminis, in which the sperm accumulates; mature males have elongate genital papillae on these segments. A pseudocopulation apparently takes place in these species.

196 Parapodia of all following body segments well developed, of the same type. They are uniramous, with large, leaf-shaped, dorsal and ventral cirri; podial lobe usually elongate, conical and often with 1 or 2 cirriform terminal appendages. Setae very thin and long, simple or complex (segmented); at the base of the bundle of setae, in its lower part, are sometimes also several shorter acicular setae. At the base of the parapodia are large, convex podial glands and chromatophores with dark pigment; the chromatophores are luminescent, probably to attract the opposite sex. Pygidium with 1 or 2 anal cirri.

All Alciopidae are pelagic. Most of them have a delicate, semitransparent body, which makes them invisible in the water, and only their large telescopic eyes indicate their presence. Dark transverse spots are present on the dorsal side in some species, mainly on the anterior segments, producing a variegated coloration.

There is a lack of uniformity in the names of the genera of Alciopidae. Støp-Bowitz (1948) recently proposed different names from those given by Fauvel (1923) for nearly all genera because of priority and nomina praeoccupata. Thus, out of the 8 genera listed by Fauvel, only one retained its old name, Vanadis, in Støp-Bowitz's nomenclature. Such a radical change of generic names of old standing (dementia nomenclatorica) makes systematic work very difficult, but practically all later authors accepted the classification of Støp-Bowitz, and it is also accepted here. Below is a list of the generic names of Fauvel and of Støp-Bowitz:

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* Translation: of mighty or strong appearance, which well describes the frightening impression these species make with their enormous telescopic eyes.

After Fauvel	After Støp-Bowitz
Alciopa Aud. and M.-Edw., 1833	Naiades Delle Chiaje, 1830
Vanadis Claparède, 1870	Vanadis Claparède, 1870
Greeffia McIntosh, 1885	Alciopa Aud. and M.-Edw., 1833
Asterope Claparède, 1870	Torrea Quatrefages, 1850
Callizonella Apstein, 1891	Krohnia Quatrefages, 1865
Corynocephalus Levinsen, 1885	Alciopina Claparède and Panceri, 1867
Rhynchonerella Costa, 1882	Plotohelmis Chamberlin, 1919
Callizona Greeff, 1876	Rhinchonerella Costa, 1862

Støp-Bowitz adds to the above list the new genus Watelio Støp-Bowitz. The insufficiently described genus Mauita Chamberlin (1919a), with only the species M. nans, should probably be united with the genus Vanadis Claparède; according to Dales (1959: 123); the only difference between them is that the first 2 segments are fused in Mauita, so that 2 pairs of tentacular cirri are apparently situated on the 1st segment.

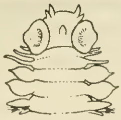
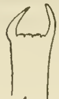
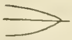
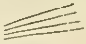
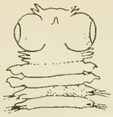
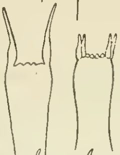
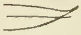
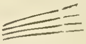
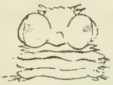
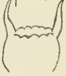
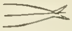
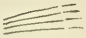
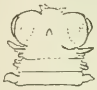
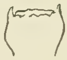
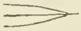
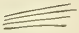
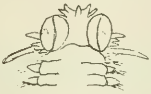
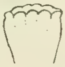
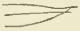
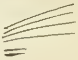
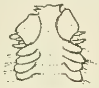
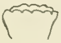
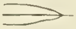
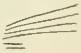
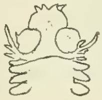
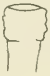
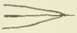
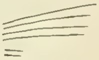
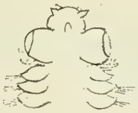
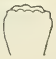
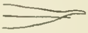
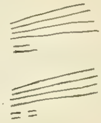
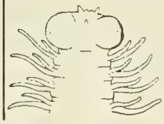
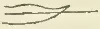
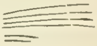
Two distinct groups of genera can be distinguished in the family Alciopidae.

1. There is only one pair of tentacular cirri on all circumoral segments; some segments in the anterior part of the body have rudimentary parapodia without setae; females with 1 or 2 pairs of sperm pockets ("seminal receptacles") formed by the modified dorsal cirri of the anterior parapodia; all setae of the same type (either simple or segmented): genera Torrea Quatrefages, Naiades Delle Chiaje and Vanadis Claparède.

2. Two pairs of tentacular cirri on the 2nd and 3rd segments (or only on
197 the 3rd segment); segments with rudimentary parapodia absent in the anterior part of the body; females without "seminal receptacles"; setae of two types, hairlike, simple setae or segmented, acicular setae; genera Alciopina Claparède and Panceri, Plotohelmis Chamberlin, Krohnia Quatrefages, Rhynchonerella Costa, Alciopa Aud. and M.-Edw. and Watelio Støp-Bowitz.

The main characters for the classification are given in the following table.

In their general structure, the Alciopidae closely resemble the Phyllodocidae; we consider them as a collateral branch of benthic Phyllodocidae of
198 the group Eulalia, which have become pelagic (p. 66). The adaptation of the Alciopidae to a planktonic life took place by transformation of the podial cirri into natatorial appendages and development of very complex, hypertrophied eyes, which enable them to find their prey. The proboscis has become very complicated: cirriform processes with numerous gland cells secreting mucus developed at its distal end; this type of proboscis is certainly able to catch small planktonic crustaceans. The seminal receptacles which developed in the females should also be considered as adaptations to a planktonic life, because the sparse populations of Alciopidae make the finding of the opposite sex difficult.

Genus	Cephalic end	Proboscis	Tentacular cirri	Recept. seminis	Podial lobe	Setae
Torrea			1+1+1	Present		
Vanadis			1+1+1 $1+1+\frac{1}{1}$	"		
Alciopa			"	"		
Naiades			1+1+1	"		
Krohnia			$1+\frac{1}{1}+\frac{1}{1}$	Absent		
Alciopina			"	"		
Plotohelmis			$1+\frac{1}{1}+\frac{1}{N}$ $1+\frac{1}{1}+\frac{1}{1}$	"		
Rhynchonerella			$1+\frac{1}{1}+\frac{1}{1}$	"		
Watelio				"		

The relationships in the family Alciopidae are represented in Figure 20 (p. 62). The primitive form is the genus Rhynchonerella in Dales' opinion (1955b), the species of which resemble benthic Phyllodocidae in many respects. Their proboscis still has no cirriform appendages and seminal receptacles are absent. The most specialized and highly adapted forms are Vanadis and Torrea. The genus Watelio has an intermediate position between the two groups of Alciopidae.

Species of Alciopidae occur mainly in the open ocean (holopelagic forms), chiefly in warm tropical waters. The following genera have been found in the Northwest Pacific near the Kuril Islands (material of Soviet expeditions):

Vanadis Claparède, Alciopa Aud. and M.-Edw., Alciopina Claparède, Krohnia Quatrefages, Rhynchonerella Costa.

Many species of Alciopidae have a very wide distribution. The usual plankton-collecting methods usually produce only fragments, but the species can be determined by the structure of the cephalic end.

Key to genera of the family Alciopidae

1 (6). Several segments with rudimentary parapodia in the anterior part of the body.
2 (3). Setae simple, hairlike . . . . . 2. **Naiades** Delle Chiaje (p. 190)
3 (2). Setae segmented, with slender distal part.
4 (5). Podial lobe without cirriform appendages . . . . 1. **Torrea** Quatrefages (p. 188)
5 (4). Podial lobe with one cirriform appendage . . . . 3. **Vanadis** Claparède (p. 190)
6 (1). Segments with rudimentary parapodia in anterior part of body absent.
7 (8). Podial lobe with 2 cirriform appendages. Setae of one type: thin, long, segmented . . . . . . 4. **Alciopa** Aud. and M.-Edw. (p. 193)
8 (7). Podial lobe without cirriform appendages, or with only one. Setae of 2 types, several shorter acicular setae and simple hairlike segmented setae in lower part of bundle.
199 9 (12). Setae simple, hairlike and acicular.
10 (11). Podial lobe with one cirriform appendage . . . . 7. **Krohnia** Quatrefages (p. 196)
11 (10). Podial lobe without cirriform appendage . . . . 6. **Alciopina** Claparède (p. 195)
12 (9). Setae segmented and acicular.
13 (14). Podial lobe without cirriform appendage . . . . 5. **Plotohelmis** Chamberlin (p. 194)
14 (13). Podial lobe with one cirriform appendage.
15 (16). Aciculum extending slightly beyond podial lobe . . . . 8. **Rhynchonerella** Costa (p. 198)
16 (15). Aciculum very large, extending distinctly beyond podial lobe . . . . 9. **Watelio** Støp-Bowitz (p. 200)

1. Genus **TORREA** Quatrefages, 1850

(Liocapa Costa, 1862; Asterope Claparède, 1870)

Proboscis cylindrical, long, with 2 lateral cirriform processes at the distal end. Three pairs of tentacular cirri on the 3 anterior circumoral segments. Formula: 1 + 1 + 1. First two body segments with rudimentary parapodia. Dorsal cirri on first 2 body segments transformed into large seminal pockets in females. Parapodia with large, leaf-shaped, dorsal and ventral cirri; podial lobe without finger-shaped appendage. All setae of the same type: segmented, with elongate, awl-shaped distal part. Podial glands large, pigmented. Two anal cirri.

Type species: Alciopa candida Delle Chiaje, 1841.

Only 2 species in this genus.

Key to species of the genus *Torrea* Quatrefages

1 (2). Distal margin of proboscis with small marginal papillae between lateral cirriform processes . . . . 1. **T. candida** (Delle Chiaje)
2 (1). Distal margin of proboscis smooth (without papillae), between lateral cirriform processes . . . . *****T. pelagica** Chamberlin, 1919
Chamberlin, 1919a: 131–133, pl. 24, figs. 4–9; Dales, 1957:111.
Isolated records from the Northwest and Southeast Pacific

1. **Torrea candida** (Delle Chiaje, 1841) (Plate XXIII, Figures 1–4)

Quatrefages, 1865: Vol. II, 159–160, pl. IV, figs. 6–7, pl. IX, figs. 15–16 (*Torea vitrea*); Greeff, 1876a: 62–65, pl. II, figs. 7–13, pl. III, figs. 22–27 (*Asterope*); Hering, 1892: 747, pl. V (*Alciopa vittata*); Izuka, 1914: 2–3, pl. I, fig. 10 (*Asterope*); Fauvel, 1923: 202–203, fig. 75, a–d (*Asterope*); Monro, 1930: 82; 1936: 119; Wesenberg-Lund, 1939: 22–25, map 13, figs. 17–18; Støp-Bowitz, 1948: 22–23, figs. 13, 14; Dales, 1957: 111, figs. 14–16.

Single cephalic tentacle in the form of a small tubercle; paired cephalic 200 tentacles oblong, upper tentacles distinctly shorter than lower tentacles. Eyes dark reddish brown; lenses directed laterally; distance between eyes less than their width.

Proboscis very long, as long as 12 anterior segments or longer; 2 long lateral cirriform processes at anterior end of proboscis, and between them 4–5 short marginal papillae; the papillae are trilobed, the middle lobe longer than the others.

First pair of tentacular cirri situated at level of eyes, the other two pairs behind the eyes; tentacular cirri of first and second pairs connected by an undulate fold on the ventral side. First two body segments differing distinctly from the other segments; dorsal cirri on first two body segments either markedly reduced (in males) or forming very large vesiclelike seminal pockets (in females).

Parapodia, from 3rd body segment onward, with lanceolate dorsal cirrus and a slightly smaller, oval ventral cirrus; podial lobe conical, aciculum projecting outside and with a bundle of thin, long segmented setae. A large pigmented podial gland on dorsal side of each parapodium. On the following 10–15 segments, from the 3rd body segment onward, pigmentation of podial glands extending to the dorsal side, forming a characteristic transverse pattern (transverse stripes) on the transparent body. Number of segments to 270; length 150–250 mm, width 2–3 mm.

Distribution. The ZIN collection contains specimens from the Mediterranean. Widely distributed: Atlantic and Indian oceans, Mediterranean; recorded from the Pacific off the coasts of Japan and California (common in California); usually in the surface layers.

2. Genus **NAIADES** Delle Chiaje, 1830

Proboscis short, with 2 small lateral cirriform processes. Three pairs of tentacular cirri on the 3 circumoral segments. Formula: 1 + 1 + 1. First 3 body segments with rudimentary parapodia with only one aciculum; dorsal and ventral cirri of females on 2nd (? or 1st) body segment transformed into large seminal pockets. Dorsal and ventral cirri leaf-shaped. Podial lobe without finger-shaped appendage. Setae simple, hairlike. Podial lateral glands pigmented.

Type species: Naiades cantrainii Delle Chiaje, 1830.

Monotypic genus.

1. **Naiades cantrainii** Delle Chiaje, 1830 (Plate XXIII, Figures 5, 6)

Greeff, 1876a: 57–60, pl. II, figs. 1–4, pl. III, figs. 14–18 (Alciopa); Viguier, 1886: 404–405, pl. XXIV, figs. 1–5 (Alciope microcephala); Apstein, 1900: 7–8, pl. V, fig. 53 (Alciopa); Izuka, 1914: 2–3, pl. I, fig. 9 (Alciopa); Fauvel, 1923: 203–204, fig. 70, a–c (Alciopa): Monro, 1936: 115 (Alciopa); Wesenberg-Lund, 1939: 25–28, map 13, fig. 19 (Alciopa); Treadwell, 1943: 35, pl. I, figs. 16, 17, pl. II, fig. 18 (Alciopa distorta); Støp-Bowitz, 1948: 24–25, fig. 15–16; Dales, 1957: 113–115, figs. 18–19; Tebble, 1960: 257; 1962: 388–389.

201 Single cephalic tentacle small, ovoid, situated near anterior margin; paired cephalic tentacles spindle-shaped, small, of the same size. Eyes red; lenses directed laterally and slightly anteriorly. Proboscis short, with trilobed small, marginal papillae and 2 lateral cirriform processes which are only slightly longer than the marginal papillae. First pair of tentacular cirri below the eyes larger than the other 2 pairs and connected ventrally by an undulate fold; 2nd and 3rd pair of tentacular cirri very small (often indistinct). First three body segments markedly reduced (podial lobe very small, usually without setae); podial cirri of 2nd body segment of females transformed into vesiclelike seminal pockets. Parapodia, from 4th body segment onward, with an elongate dorsal cirrus and a shorter ventral cirrus; podial lobe conical, very elongate, with an aciculum which projects distinctly outside, and with a bundle of long, thin, hairlike, simple setae. Podial glands large, distinct, dark brown. Body transparent. Number of segments 70–120. Length 40–110 mm, width 2–5 mm.

Distribution. The ZIN collection contains specimens from the Mediterranean. Widely distributed in warm waters, mainly in the surface layers in the Atlantic, Indian and Pacific oceans; occurs near the coast of Japan and California.

3. Genus **VANADIS** Claparède, 1870

(Cleta Claparède, 1870)

Proboscis cylindrical, long, with 2 large lateral cirriform processes resembling tentacles, or with a shorter proboscis, with only one ring of pointed papillae of uniform size at the distal end. Three or 4 pairs of tentacular cirri. Formula: 1 + 1 + 1 and $1 + 1 + \frac{1}{1}$. Anterior body segments (4th –10th) usually with rudimentary (underdeveloped) parapodia without setae. Dorsal cirri of females on one or two anterior body segments transformed into large seminal pockets. Dorsal and ventral cirri on normal parapodia leaf-shaped, large. Podial lobe ending in a single finger-shaped process. All setae of the same type: segmented, with thin distal part. Podial glands large, pigmented. One or 2 anal cirri.

Type species: Vanadis formosa Claparède, 1870.

The genus contains more than 10 species. Five species have been recorded from subtropical regions of the North Pacific.

Remarks. The number of tentacular cirri has been described differently for the same species because some authors include in the number of tentacular cirri some of the podial cirri on the underdeveloped parapodia of the anterior body segments, which differ little in form from the tentacular cirri. Thus, Izuka (1914) states that there are 10 pairs of tentacular cirri in V. grandis Izuka (= V. longissima (Levinsen)), but they apparently have only 3 pairs; the others are underdeveloped podial cirri. The number of underdeveloped parapodia is difficult to determine because there are gradual transitions, and the setae may be lost.

202 Key to species of the genus Vanadis Claparède

1 (8). Proboscis with lateral cirriform appendages.

2 (3). Proboscis with 2 pairs of cirriform appendages; 4 pairs of tentacular cirri . . . . * **V. tagensis** Dales (Plate XXIV, Figure 10)

Dales, 1955a: 436–439, fig. 1, a–c; Tebble, 1962: 394–395, fig. 9.
North Pacific, abyssal

3 (2). Proboscis with one pair of cirriform appendages; 3 pairs of tentacular cirri.

4 (5). Cephalic lobe with 4 cephalic tentacles . . . . * **V. minuta** Treadwell (Plate XXIV, Figures 11, 12)

Treadwell, 1906: 1158–1159, figs. 25–28; Dales, 1957: 119–121, figs. 28–30; Tebble, 1962: 390–391, fig. 7.
Subtropical and tropical regions of the Pacific

5 (4). Cephalic lobe with 5 cephalic tentacles.

6 (7). First 2 body segments with reduced parapodia . . . . 1. **V. formosa** Claparède

7 (6). First 6–9 body segments with reduced parapodia . . . . * **V. crystallina** Greeff (Plate XXIV, Figures 7–9)

Dales, 1957: 118–119, figs. 25–27.
Widely distributed in temperate and tropical regions of the Atlantic and Pacific

8 (1). Proboscis without cirriform appendages; 10–12 small marginal papillae of equal size at distal end of proboscis . . . . 2. **V. longissima** (Levinsen)

1. **Vanadis formosa** Claparède, 1870 (Plate XXIV, Figures 1, 2)

Greeff, 1876a: 67, pl. III, figs. 33–34 (V. pelagica); Apstein, 1900: 8, pl. I, figs. 1–6; Southern, 1911: 2–3; Chamberlin, 1919: 134–135; Fauvel, 1923: 205–206, fig. 77, a–c; Monro, 1930: 81; 1936: 116; Wesenberg-Lund, 1939: 28–32, figs. 20–21, map 15; Støp-Bowitz, 1948: 25–26, fig. 17; Dales, 1957: 117, figs. 21–24; Tebble, 1960: 185–186, 252–255, fig. 49; 1962: 389–390, fig. 40.

Proboscis long, cylindrical, 2 elongate lateral cirriform processes and small 3-lobed papillae at its distal end. Three pairs of tentacular cirri, the first pair larger than the other 2 pairs and connected on the ventral side by a cuticular fold. First one or two segments behind the tentacular cirri with rudimentary parapodia without setae. Dorsal cirri of 4th and 5th segments of females transformed into large seminal pockets. All following segments with elongate podial lobes with finger-shaped processes and an aciculum which projects outside; dorsal podial cirri elongate-heart-shaped, ventral cirri shorter and oval. Setae long and thin, with long, thin distal part. Podial glandular organs present on all except the most anterior segments; these organs are convex, dark, distinct. Body semitransparent. Number of segments (according to the literature) to 200 or more. Length to 200–300 mm, width 5–6 mm.

203 Distribution. One specimen from the North Pacific – 39°44' N, 151°53' E, horizon 0–50 m. Widely distributed, mainly in warm, surface waters in the Atlantic, Indian and Pacific oceans.

2. **Vanadis longissima** (Levinsen, 1885) (Plate XXIV, Figures 3–6)

Levinsen, 1885: 330–331, figs. 7–10 (Rhynchonerella); Apstein, 1900: 1, pl. I, figs. 8–9; Izuka, 1914: 5–7, pl. I, figs. 1–7 (V. grandis); Fauvel, 1923: 207, fig. 77, f–g; Monro, 1930: 79–80, fig. 24; Ushakov, 1957: 275–277, fig. 4, a–d, map 2 (V. pacifica); Dales, 1957: 121–123, figs. 31–33; Tebble, 1960: 187–188, 224, fig. 27; 1962: 392–394, figs. 8, 38; Pettibone, 1963: 91–93, fig. 22.

Proboscis without elongate lateral cirriform processes, with 10–12 pointed marginal papillae at the distal end. Three pairs of tentacular cirri of about the same length. Parapodia of anterior segments partly underdeveloped; setae usually absent on 1st body segment. Dorsal cirri on 2nd and 3rd parapodia of mature females transformed into large seminal pockets. Parapodia well developed from the 8th–9th segment onward: podial lobe elongate, with a small finger-shaped process and an aciculum, which projects outside; dorsal and ventral podial cirri elongate, dorsal cirri larger than the ventral but distinctly shorter than the podial lobes. Setae long and thin, with elongate distal part. Lateral, intensely pigmented podial glandular organs not present on all segments, segments with such organs alternating with segments without them (order of alternation varying). Segments with podial glandular organs dark brown, other segments light, so that there is a striking variegated transverse pattern. Number of segments to 200. Length 120–200 mm, width 1–2 mm.

Distribution. Our collection contains 2 fragments from the Northwest Pacific (38°21' N, 151°57' E, horizon 0–100 m). Widely distributed, mainly in tropical and subtropical regions of the Atlantic, Indian and Pacific oceans; to the Antarctic convergence in the south.

4. Genus **ALCIOPA** Audouin and Milne-Edwards, 1833

(Halodora Greeff, 1876; Nauphanta Greeff, 1876; Greeffia McIntosh, 1885)

Proboscis short, with 2 thin cirriform processes at the distal end. Three or 4 pairs of tentacular cirri. Formula: $1 + 1 + 1$ and $1 + 1 + \frac{1}{1}$. Parapodia on anterior body segments fully developed. Ventral cirri of females on anterior segments transformed into seminal pockets. Dorsal and ventral cirri large and leaf-shaped (the dorsal cirri partly cover the dorsum). Podial lobe with 2 finger-shaped processes. Parapodia with numerous thin, segmented setae, with elongate distal part. Podial glandular organs large, pigmented,
204 forming 2 ridges (a dorsal and a ventral). Compared with most other Alciopidae, the body is relatively short and broad.

Type species: Alciopa reynaudii Aud. and M.-Edw., 1833.

Many species which are now considered to belong to other genera have in the past been described under the generic name Alciopa (Hartman, 1959). There is much confusion on the synonymy and description of A. reynaudii Aud. and M.-Edw. (Nauphanta celox Greeff, 1876). The original description stated that there are 4 pairs of tentacular cirri, but Støp-Bowitz (1948) doubts this and considered Greeffia oahuensis McIntosh, for which only 3 pairs of tentacular cirri are described, as a synonym of A. reynaudii. He accordingly changed the diagnosis of A. reynaudii Aud. and M.-Edw., which in his opinion has only 3 pairs of tentacular cirri. This was accepted by Dales (1956, 1957) and Tebble (1960). However, my specimens from the Northwest Pacific have definitely 4 pairs of tentacular cirri, as stated in the original description of Alciopa reynaudii Aud. and M.-Edw. (= Nauphanta celox Greeff). I therefore consider A. reynaudii Aud. and M.-Edw. and A. oahuensis (McInt.) as different species. The genus contains only 3 species.

Key to species of the genus Alciopa Audouin and Milne-Edwards

1 (2). One pair of eyes, with an additional pair of rudimentary eyes below it . . . . ★**A. quadrioculata** McIntosh, 1885
Pacific Ocean, Hawaii
2 (1). Rudimentary eyes absent.
3 (4). Four pairs of tentacular cirri. . . 1. **A. reynaudii** Aud. and M.-Edw.
4 (3). Three pairs of tentacular cirri . . . . . ★**A. oahuensis** (McIntosh, 1885)
Atlantic, Mediterranean, Pacific

1. **Alciopa reynaudii** Audouin and Milne-Edwards, 1833 (Plate XXV, Figures 1–4)

Audouin and Milne-Edwards, 1834: 214–216, pl. V, figs. 6–11; Greeff, 1876a: 69, pl. III, figs. 40–42, pl. IV, figs. 43–55 (Nauphanta celox); Apstein, 1900: 12, pl. II, fig. 10 (Greeffia celox); Chamberlin, 1919a: 139–140 (Halodora); Southern, 1911: 3 (Greeffia celox); Fauvel, 1923: 208, fig. 78, a–c (Greeffia celox); Dales, 1957: 124–125, figs. 34–35 (synonymy).

Anterior margin of cephalic lobe slightly undulate (festooned). Frontal cephalic tentacles conical, pointed, of about the same size; median single tentacle forming a small, low tubercle. Eyes large, spherical, their lenses directed laterally and ventrally. Proboscis in our specimen retracted, but 2 long, cirriform appendages project from the mouth (see Plate XXV, Figure 1). Four pairs of short tentacular cirri, the first 3 spindle-shaped, the 4th leaf-shaped. All parapodia on the body well developed. Podial lobe
205 conical, with 2 small finger-shaped processes at the distal end. A large aciculum, situated between the finger-shaped appendages, projects slightly outside. Dorsal and ventral cirri very large, leaf-shaped, rounded, of about the same size, with fine punctate brown pigmentation. Last segment markedly reduced. One anal cirrus on the ventral side of the anal lobe. Podial glandular organs large, consisting of two distinct formations: a dark, strongly pigmented dorsal transverse ridge, and a lighter ventral ridge. Setae numerous, thin, segmented, with long distal part. A few small, thin, simple setae (without the distal part) in the lower part of the bundle are recognizable only by close examination. This has not been described for this species in the past.

Number of segments 48; length 35 mm, width including the parapodia 9 mm, without the parapodia 4 mm (according to the literature: length to 60 mm, width to 12 mm).

Distribution. Described from a female from the Northwest Pacific 46°06' N, 170°00' E. Recorded from the Atlantic, Indian and Pacific oceans. Recorded north of San Francisco (Dales, 1957).

5. Genus PLOTOHELMIS Chamberlin, 1919

(Rhynchonerella Costa, 1862, part.)

Proboscis without lateral cirriform processes, only with small marginal papillae at the end. Four or 5 pairs of tentacular cirri. Formula $1+\frac{1}{1}+\frac{1}{N}$ and $1+\frac{1}{1}+\frac{1}{1}$. Parapodia well developed on all body segments. Seminal receptacles not observed. Dorsal podial cirri larger than ventral cirri. Podial lobe without finger-shaped appendage. Setae of two types: simple acicular and segmented, with thin, awl-shaped distal part. Podial glands not always distinct. Two anal cirri.

Type species: Plotohelmis alata Chamberlin, 1919.

The genus contains 3 species: Plotohelmis alata Chamberlin, 1919, Pl. capitata (Greeff, 1876) and Pl. tenuis (Apstein, 1900), which differ only slightly in the length of the tentacular cirri (Dales, 1957); the ZIN collection has only a specimen of Pl. tenuis (Apstein).

1. Plotohelmis tenuis (Apstein, 1900) (Plate XXV, Figures 5–7)

Apstein, 1900: 14, pl. 2, figs. 14–16 (Corynocephalus); ? Izuka, 1914: 8–9, pl. I, figs. 11–12 (Rhynchonerella fulgens); Chamberlin, 1919a:

141 (Corynocephalus); Dales, 1957: 125–128, figs. 36–39; Tebble, 1962: 403–404.

Frontal tentacles short, lanceolate; median single tentacle slightly larger than the frontal tentacles. Eyes very large. Five pairs of tentacular cirri on the 3 circumoral segments. Formula: $1+\frac{1}{1}+\frac{1}{1}$; dorsal cirri on 2nd and 3rd circumoral segments the longest; ventral cirri short, indistinct. Dorsal cirri on body segments large, long, leaf-shaped; ventral cirri small, smaller
206 than the podial lobe, which is conical, without finger-shaped appendages, with a large aciculum projecting outside. Only acicular setae on the first body segments (to 12 on one parapodium), numerous thin, long, segmented setae and one acicular seta in the lower part of the bundle on the following segments. Podial glandular organs reddish brown; they are indistinct on the anterior segments. Number of segments to 80; length to 25 mm.

Distribution. The ZIN collection contains only one badly preserved specimen from Hainan. According to the literature, it occurs in the Atlantic Ocean and in the Mediterranean; Pacific Ocean north to 50° N; it occurs mainly in tropical and subtropical regions.

6. Genus **ALCIOPINA** Claparède and Panceri, 1867

(Corynocephalus Levinsen, 1885)

Proboscis short, smooth or with small, rounded papillae of uniform size at the distal end; lateral elongate processes absent. Five pairs of tentacular cirri on the 3 anterior (circumoral) segments, one pair on the 1st segment, two pairs on each of the 2nd and 3rd segments. Formula: $1+\frac{1}{1}+\frac{1}{1}$. Rudimentary parapodia absent in anterior part of body. Seminal receptacles not observed. Podial lobe without finger-shaped process at the distal end. Podial dorsal and ventral cirri leaf-shaped, large. There are only simple setae, but in the lower part of the bundle, which consists of long, thin, hair-like setae, there are several shorter and thicker acicular setae. Podial pigmented glands present. Pygidium with 2 anal cirri. Body relatively short.

Remarks. According to Levinsen (1885), there are only 4 pairs of tentacular cirri; the lower tentacular cirri on the 3rd segment are so small that Levinsen may have overlooked them.

Type species: Alciopina parasitica Claparède and Panceri, 1867. Monotypic genus.

1. **Alciopina parasitica** Claparède and Panceri, 1867 (Plate XXV, Figures 8–11)

? Apstein, 1893: 148, pl. V, figs. 13–14 (Corynocephalus gazellae); Apstein, 1900: 14, pl. II, figs. 17–18 (Corynocephalus albomaculatus); Chamberlin, 1919a: 141–143, pl. 23, figs. 1–3 (Corynocephalus paumotanus); Fauvel, 1923: 208–209, fig. 78, d–i (Corynocephalus albo-maculatus); Treadwell, 1943: 37 (Corynocephalus paumotanus); Støp-Bowitz, 1948: 32, Ushakov, 1957: 277–278, fig. 4, e–h, map 2 (Corynocephalus paumotanus); Dales, 1957: 128–129.

Cephalic lobe rounded anteriorly. Median single cephalic tentacle short, small and thick; paired tentacles large. Eyes directed laterally. Proboscis about as long as the 3 anterior segments. First pair of tentacular cirri shorter than the dorsal pair of tentacular cirri on the 2nd segment, and these are shorter than the dorsal pair on the 3rd segment; ventral tentacular cirri on the 2nd and 3rd circumoral segments very small, particularly on the 3rd segment, much shorter than the first pair of tentacular cirri.
207 Podial lobe on body segments conical, without finger-shaped process at the distal end; aciculum extending beyond podial lobe. Podial dorsal and ventral cirri very large, particularly the dorsal cirri, which are heart-shaped. Dorsal podial cirri in middle of body overlapping and completely covering the dorsum (like the dorsal scales in the Aphroditidae). Setae simple, but are thin and hairlike and others are coarse and thick, acicular; there are some 2–3 acicular setae on each of the 4 or 5 anterior segments, and then their number decreases to one on each parapodium; hairlike setae numerous from the 5th–6th segment onward. Acicular setae slightly curved. Podial glandular organs dark on the dorsal side. Body colorless, semitransparent.

Number of segments to 50; length to 30 mm, width to 3.7 mm (our specimens are not complete).

Distribution. The ZIN collection has 2 specimens from the Northwest Pacific – 34° N, 148°49' E; 30°30' N, 138° E. Widely distributed, mainly in warm regions of the Pacific, but it occurs also in the Atlantic and, possibly, in the Indian Ocean.

7. Genus **KROHNIA** Quatrefages, 1865

(Callizonella Apstein, 1890; nec Krohnia Langerhans, 1880 (Chaetognatha))

Proboscis short, with small marginal papillae, without long lateral cirriform processes. Five pairs of tentacular cirri on the 3 anterior (circumoral) segments, one pair on the 1st segment, two pairs on the 2nd and 3rd segments. Formula: $1+\frac{1}{1}+\frac{1}{1}$. Rudimentary parapodia absent in anterior part of body. Seminal receptacles not observed. Dorsal and ventral podial cirri leaf-shaped and large. Podial lobe with a finger-shaped process at the end. Setae simple, thin, hairlike, but thicker and shorter, simple acicular setae are also present on the anterior segments and in the lower part of the bundles on other segments. Podial glands large. Pygidium with one anal cirrus.

Type species: Alciopa lepidota Krohn, 1845.

The genus contains 2 species.

Key to species of the genus Krohnia Quatrefages

1 (2). Dorsal tentacular cirri on the 3rd circumoral segment very large, much longer than the long dorsal tentacular cirri on the 2nd segment . . . . 1. **K. lepidota** (Krohn)

2 (1). Dorsal tentacular cirri on 3rd segment small, of same size as the dorsal tentacular cirri on the 2nd segment . . . . 2. **K. excellata** (Uschakov)

1. **Krohnia lepidota** (Krohn, 1845) (Plate XXVI, Figures 1–4)

Krohn, 1845: 175 (Alciopa); Apstein, 1900: 12–13, pl. II, figs. 11–13 (Callizonella); Chamberlin, 1919a: 146–147 (Rhynchonerella); Fauvel, 1923: 211–212, fig. 79, e–h (Callizonella); Wesenberg-Lund, 1939: 38–
208 40, fig. 25 (Callizonella); Treadwell, 1943: 38, pl. II, fig. 25 (Callizonella pigmenta); Støp-Bowitz, 1948: 33; Ushakov, 1957: 278, fig. 5, map 2 (Callizonella); Dales, 1957: 129; Tebble, 1962: 406–407, fig. 18.

Frontal tentacles large, pointed. Lenses of eyes directed laterally and slightly ventrally. Marginal papillae at distal end of proboscis small, of uniform size. Upper tentacular cirri of 3rd segment very long and much larger than the other tentacular cirri (longer than the width of the body). Parapodia well developed on all body segments. Dorsal podial cirri very large, broadly leaf-shaped, with small, pointed, papilliform end; ventral podial cirri also leaf-shaped with pointed end, but smaller than the dorsal cirri. Podial lobe elongate, with a finger-shaped appendage at the distal end and a large aciculum projecting outside. All setae simple, but of two types: some setae very thin, hairlike, others coarser and acicular. The latter predominate on the anterior segments, their number decreasing posteriorly, only one acicular seta on a parapodium on the posterior segments. Podial glandular organs dark. Body semitransparent, with numerous dark spots, which form 2 longitudinal stripes on the ventral side; margins of dorsal and ventral cirri dark. Number of segments 100–120. Length to 100 mm.

Distribution. Described from the Northwest Pacific – 34°02' N, 148°49' E and 38°21' N, 151°57' E. Widely distributed in tropical and subtropical regions of the Atlantic and Pacific oceans.

2. **Krohnia excellata** (Uschakov, 1955) (Plate XXVI, Figures 5–7)

Ushakov, 1955a: 108, fig. 11, g–d (Callizonella)

Cephalic tentacles short and thick. Eyes directed anteriorly and slightly laterally. Proboscis with 12 round marginal papillae of uniform size at the distal end; pharynx tuberculate. Tentacular cirri short, spindle-shaped, with pointed end. Dorsal tentacular cirri of 3rd segment the longest, but less than half as long as the body is wide; ventral tentacular cirri of 2nd and 3rd segments about half as long as the dorsal cirri and as long as the tentacular cirri of the 1st segment. Ventral tentacular cirri of 3rd segment markedly flattened, resembling the ventral podial cirri. Parapodia well developed on all setose segments. Dorsal and ventral podial cirri leaf-shaped, elongate, with pointed end; dorsal cirri larger than ventral cirri; dorsal cirri of the 5–10 anterior segments shorter and broader than on the following segments; lower part of dorsal cirri (near the podial lobe) thick in mature specimens. Podial lobe elongate, with a finger-shaped process at the distal end, and with a large aciculum. All setae simple, long and hairlike, more than 50 in a bundle; there are also 2 or 3 thicker and shorter,
209 acicular setae on the middle segments. Podial glandular organs convex, surrounding the base of the parapodia dorsally and posteriorly, more weakly developed on the anterior segments. Coloration of dorsum brown, darker on the anterior segments; dorsal and ventral podial cirri light, weakly punctate;

podial organs dark brown, almost black; cephalic lobe dark anteriorly, cephalic tentacles colorless; eyes reddish brown. More than 100 segments; length over 70 mm, width to 6 mm. Eggs present in podial lobe and at base of dorsal cirrus.

Distribution. The ZIN collection has 3 specimens from the Northwest Pacific near the Kuril Islands (collected with a pelagic net, depth 4000–0 and 500–0 m) and a specimen from the southwestern Bering Sea ("Vityaz," station 1418).

Genus **RHYNCHONERELLA** Costa, 1862

(Callizona Greeff, 1862)

Proboscis short, without long lateral cirriform processes, with small papillae of uniform size at the distal end. Five pairs of tentacular cirri on the 3 anterior (circumoral) segments. Formula: $1+\frac{1}{1}+\frac{1}{1}$. Rudimentary parapodia absent in anterior part of body. Seminal receptacles not observed. Dorsal and ventral podial cirri leaf-shaped. Podial lobe with a terminal finger-shaped process. Dorsal setae thin, segmented, with long, thin distal part; ventral setae thick and short, simple or complex, acicular. Podial glandular organs pigmented. One or 2 anal cirri.

Type species: Rhynchonerella gracilis Costa, 1862.

This genus contains 7 species, but only 4 have been recorded from the northern regions of the Pacific and Atlantic.

Key to species of the genus Rhynchonerella Costa

1 (4). Acicular setae simple.
2 (3). One or two thick, short setae and numerous thin, segmented setae on each parapodium; acicular setae smooth . . . . 1. **Rh. gracilis** Costa
3 (2). Only 3–6 thick, short, simple setae on the 5–10 anterior parapodia; thin, segmented setae and one serrate acicular seta on the following segments . . *Rh. mobii (Apstein, 1893) (Plate XXVII, Figures 10–13)
Apstein, 1900 : 16–17, pl. III, figs. 23–30 (Callizona); Fauvel, 1923 : 213–214, fig. 80, a–d (Callizona); Støp-Bowitz, 1948 : 34; Dales, 1957 : 131–132, figs. 39–43; Tebble, 1962 : 396–398, fig. 11.
Atlantic and Pacific, tropical and subtropical regions
4 (1). Acicular setae segmented.
5 (6). Upper tentacular cirri of 3rd segment short; acicular setae with thin,
210 smooth distal part . . . . 3. **Rh. angelini** (Kinberg)
6 (5). Upper tentacular cirri of 3rd segment long (much longer than all the others); acicular setae with slightly serrate distal part . . . . 2. **Ph. petersii** (Langerhans)

1. **Rhynchonerella gracilis** Costa, 1862 (Plate XXVII, Figures 1–4)

Greeff, 1876a: 72, pl. 5, figs. 60–62 (Callizona nasuta); Apstein, 1900: 19, pl. III, figs. 31–32; 20, pl. V, figs. 44–50 (C. nasuta + C. henseni); Izuka, 1914: 7–8, pl. I, fig. 8 (C. japonica); Fauvel, 1923: 215–216, fig. 81, a–c (C. nasuta); Wesenberg-Lund, 1939: 42–43, figs. 27–28 (C. nasuta); Støp-Bowitz, 1948: 36, Ushakov, 1957: 279–281, fig. 6, a–d, map 2 (C. nasuta); Dales, 1957: 131; Tebble, 1962: 396, fig. 10, a, b.

Cephalic tentacles thick, elongate. Lenses of eyes directed laterally. Proboscis with 12 small marginal papillae of uniform size at the distal end. The first, shortest pair of tentacular cirri is situated on the 1st segment; each of the next two segments bears 2 pairs, the dorsal cirri distinctly larger than the ventral cirri; dorsal tentacular cirri of 2nd and 3rd segments the largest, but not longer than the width of the body. Dorsal podial cirri on all body segments slightly elongate, pointed; ventral podial cirri resembling the dorsal cirri but smaller. Podial lobe elongate, with a finger-shaped process at the distal end and an aciculum projecting outside. Setae on all segments of 2 types: numerous thin, long, segmented setae with thin, long distal part and 1 or 2 shorter and thicker, simple, acicular setae in the lower part of the bundles. Body whitish with dark brown lateral spots (glandular organs); eyes reddish. Number of segments to 100; length 30–60 mm, width 0.5–1 mm.

Distribution. Northwest Pacific, east of Honshu (34°02' N, 148°49' E and 39°22' N, 148°48' E; horizon 0–50 m, 1953). Recorded from tropical and subtropical regions of the Atlantic and Pacific oceans.

2. **Rhynchonerella petersii** (Langerhans, 1880) (Plate XXVII, Figures 5–9)

Langerhans, 1880: 312, pl. XVII, fig. 49 (Alciopa); Greeff, 1885: 449, pl. XIII, fig. 26 (Vanadis); Viguier, 1886: 405–408, pl. XXIV, figs. 6–13 (Vanadis heterochaeta); Apstein, 1900: 18, pl. IV, figs. 39–43 (Callizona setosa); Fauvel, 1923: 214, fig. 80, e–k (Callizona setosa); Støp-Bowitz, 1948: 34; Ushakov, 1957: 281, fig. 6, e–i, map 2 (Callizona setosa); Dales, 1957: 133; Tebble, 1962: 398–400, fig. 12, a–c.

Cephalic tentacles large. Lenses of eyes directed anteriorly and laterally. Proboscis with small marginal papillae of uniform size at the distal end. First pair of tentacular cirri situated on the 1st segment, dorsal cirri distinctly larger than the ventral cirri; the dorsal tentacular cirri of the 3rd segment are the longest (as long as the width of the body). Dorsal podial cirri very large, leaf-shaped, delicate; they are first heart-shaped, then
211 broadly oval. Ventral podial cirri several times smaller than the dorsal cirri, lanceolate, slightly pointed. Podial lobe elongate, with a finger-shaped process and an aciculum which projects outside at the distal end. All setae segmented, but of different form: thin, long setae with thin distal part on the anterior segments in the upper part of the bundles, thick, shorter setae with short, slightly serrate distal part (serration visible only under high magnification) in the lower part of the bundles; short, thick setae are numerous on the anterior segments; their number decreases to 1 or 2 on the middle segments. Body semitransparent, whitish yellow, with dark brown

spots at the sides of the segments (podial glandular organs); eyes dark brown. Number of segments 40–60; length 15–20 mm, width 0.5–1 mm. We examined fragments of the anterior part of the body.

Distribution. The ZIN collection has specimens from the Northwest Pacific, east of Honshu (34°02' N, 148°49' E and 39°22' N, 148°48' E, horizon 0–50 m, 1953). It occurs in tropical and subtropical regions of the Atlantic and Pacific oceans.

3. **Rhynchonerella angelini** (Kinberg, 1866) (Plate XXVIII, Figures 1–4)

Kinberg, (1866) 1910 : 56 (Krohnia); Apstein, 1900 : 18–19, pl. IV, figs. 33–38 (Callizona); Moore, 1908 : 340–341 (Callizona); Chamberlin, 1919a : 147–150, pl. 25, figs. 7–8, pl. 29, figs. 1–6 (Rhynchonerella pycnocera); Fauvel, 1923 : 215, fig. 81, d–i (Callizona); Wesenberg-Lund, 1939 : 41–42, fig. 27, map 21 (Callizona); Treadwell, 1943 : 36–37 (Rhynchonerella pycnocera); Støp-Bowitz, 1948 : 34–36, fig. 22; Berkeley and Berkeley, 1948 : 40–41, fig. 56 (Callizona); Dales, 1957 : 133, figs. 44–46; Imajima, 1961 : 8–9, fig. 3; Tebble, 1962 : 400–403, figs. 13–14, a–c.

This species is closely related to R. petersii, but differs from it mainly in the shorter tentacular cirri. Dorsal podial cirri broad, larger than the podial lobe; ventral podial cirri lanceolate, pointed, shorter than the podial lobe. Ventral short, thick, segmented setae with small, thin, smooth distal part. Podial glandular organs distinct, dark brown. Number of segments 100–150; length to 120 mm.

Distribution. The ZIN collection contains specimens from the Tasman Sea (Tebble, 1968). Recorded from tropical and subtropical regions of the Atlantic, Indian and Pacific oceans; northward to the Aleutian Islands in the North Pacific.

9. Genus **WATELIO** Støp-Bowitz, 1948

Proboscis with lanceolate papillae around its distal end, without elongate lateral cirriform appendages. Four pairs of tentacular cirri on the 3 anterior segments, shorter than the podial cirri of the body segments. Dorsal and ventral cirri of body segments elongate, pointed; ventral cirri slightly larger than the dorsal cirri. Aciculum very large (its free end as long as
212 the entire pedicel), projecting from the podial lobe; at its end is a small finger-shaped appendage, situated dorsal to the aciculum. Setae thin, long, segmented; 1 or 2 simple setae in the lower part of the bundle. Podial glandular organs present from the first segments.

Type species: Callizona gravieri Benham, 1929.

Monotypic genus.

1. **Watelio gravieri** (Benham, 1929) (Plate XXVIII, Figures 5–7)

Benham, 1929 : 190–191, pl. 1, figs. 13–17 (Callizona gravieri); Støp-Bowitz, 1948 : 37–38, fig. 32 (Watelio longifoliata); Dales, 1957 : 134–135, figs. 47–50.

Cephalic lobe broad, with 5 small tentacles. Eyes widely separated in adults. Proboscis with 12 terminal papillae. Setae may be absent on the anterior body segments. Number of segments to 190; length to 150 mm, maximum width without the parapodia 3 mm.

Not represented in the ZIN collection.

Distribution. Recorded from the Northwest Pacific (40—45° N), New Zealand region; Atlantic Ocean, south of the Azores.

III. Family Tomopteridae Grube, 1848*

A very aberrant and homogeneous family, highly specialized and adapted to planktonic life. Body transparent, parapodia without setae, with fins. The very long tentacular cirri "whiskers," directed posteriorly, are the most distinctive character.

Body divided into 3 parts: head, body and pygidium (the last sometimes absent). Cephalic lobe with one pair large, broad, tapering tentacles which are directed laterally or slightly posteriorly ("prostomal horns"). Usually 2 small eyes and 2 nuchal organs, resembling "epaulets," covered with ciliary epithelium. Pharynx short, unarmed. Cephalic lobe fused with the 2 following segments, which bear 2 pairs of tentacular cirri. Anterior cirrus small, situated on the ventral side slightly before the mouth (absent in some species and sometimes in adults); second pair very large, each cirrus with a long, rigid inner seta; tentacular cirri of second pair ("whiskers") directed slightly lateral and posteriorly, almost reaching to the posterior end.

Behind the tentacular cirri is a relatively narrow part without podial processes ("neck"). Parapodia in the body section with a long stem, ending in 2 pointed branches of about the same size which are surrounded by leaf-shaped, corrugated plates, the fins or pinnules. Parapodia without setae, acicula reduced.

213 Various types of glands are present on the podial branches and fins which are of importance in systematics. There are 4 types of glands: 1) chromophile glands, which are the largest and very distinct, consisting of a number of ducts with a common opening; these glands stain well with hematoxylin; they are present only on the ventral fins, from the 3rd or 4th pair of parapodia, and are often well visible without staining under good light; 2) hyaline glands, which are small, present on the ventral and dorsal fins, or only on one fin; they consist of small ducts, dark brown or reddish in the middle (not stained with hematoxylin); 3) rosettes, modified hyaline glands, very small, with spherical bodies in the center which contain a dark pigment that may fade after long preservation in alcohol, as in the hyaline glands; rosettes are usually present only in species with a pygidium with reduced parapodia; they are found on the first two body segments on the stem of the parapodium or on its ventral branch, clearly visible only in lateral view; they are situated on the following segments near the conical distal end of the branch; if rosettes are present, hyaline glands are absent; 4) spur glands, which are present only on the ventral fins together with chromophile glands; they stain well with hematoxylin; they are not present in all species. The rosette glands are organs of luminescence.

To 30 pairs of parapodia (not including underdeveloped parapodia on the pygidium), the number relatively constant in some species. Posterior end of body often with markedly reduced parapodia and modified into a special caudal part (pygidium).

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* Translation: with divided wings.

The gonads enter the podial processes, either into both branches or only into the dorsal branch (isolated eggs may accidentally be found in the ventral branch, which does not contain gonads, and may be mistaken for gonads).

The main characters for the determination of species are as follows: 1) presence or absence of the first pair of tentacular cirri, 2) arrangement and character of the podial glands, and 3) presence or absence of a pygidium with reduced parapodia.

All species of this family are pelagic. Parasitic stages of the narcomedusa Cunina lativentris have been found in the coelum of some species of Tomopteris (Damas, 1936).

Adult forms move by undulant movements of the fins; the second pair of tentacular cirri ("whiskers") has no locomotor function, but is a sense organ which regulates balance and floating (Schwartz, 1905).

The systematic position of the Tomopteridae is not clear. Gravier (1896) and Meyer (1926) consider them as related to the Phyllodocidae through the Alciopidae. According to Meyer, the nephridial apparatus of all these families has a very similar structure; the mesoderm of the Tomopteridae develops as two elongate primordia at the posterior end, as in Lopadorhynchus. However, the type of cephalic appendages in the Phyllodocidae and Alciopidae is different from that in the Tomopteridae. There are also important differences in the structure of the eyes (Åkesson, 1964).

214 There are only two genera in the family Tomopteridae, Enapteris Rosa and Tomopteris Eschscholtz.

Glaessner (1958) discovered well preserved imprints of polychaetes in Cambrian deposits in South Australia, the habitus of which (two horns at the cephalic end) closely resembles that of the recent Tomopteridae; he described the fossils as a new family, Sprigginidae Glaessner.

The Tomopteridae are widely distributed in the World Ocean. Wesenberg-Lund (1935, 1936, 1950c) recorded 7 species from the North Atlantic: Tomopteris helgolandica Greeff, T. nisseni Rosa, T. cavallii Rosa, T. septentrionalis Quatrefages, T. kefersteini Greeff, T. krampi Wesenberg-Lund, T. planctonis Apstein. T. helgolandica spreads with warm currents into the Barents Sea. Izuka (1914) recorded 4 species from the coast of Japan: Tomopteris pacifica Izuka, T. elegans Chun, T. septentrionalis and T. apsteini Rosa, but the last species needs confirmation as Izuka apparently had juvenile specimens. Detailed information on the composition and quantitative distribution of Tomopteris in the North Pacific was given by Dales (1955a, 1956, 1957) and Tebble (1962). Our collection contains 3 species from these areas: Tomopteris septentrionalis Quatrefages, T. elegans Chun and T. (Johnstonella) pacifica Izuka, the first being the most common. However, not all specimens can be determined to the species, since the fins, which are of great systematic importance, are often damaged after fixation.

Key to genera of the family Tomopteridae

1 (2). Podial processes surrounded by thin, leaf-shaped fins (pinnules) only on the outer surface. "Whiskers" of 2nd segment much longer than

body. . . . . *Enapteris Rosa, 1908

This genus contains only one species – E. euchaeta (Chun, 1887), described from the Mediterranean; common in warm regions of the Atlantic (Støp-Bowitz, 1948)

2 (1). Podial processes completely surrounded by thin leaf-shaped fins (pinnules). "Whiskers" shorter than body, or very slightly longer . . . . 1. Tomopteris Eschscholtz

1. Genus **TOMOPTERIS** Eschscholtz, 1825

Cephalic lobe fused with the two following segments, with a foldlike depression of varying depth anteriorly. Two large, broad tentacles ("frontal horns") at sides of cephalic lobe, which are slightly curved and directed distally. Anterior margin of tentacles thinner and more pointed than the posterior margin. Behind the tentacles, on the dorsal side, there is a small depression in which the 2 dark eyes are situated. Nuchal organs in the form of long grooves (epaulets) extend from behind the tentacles to the depressions of the eyes or slightly beyond them; the nuchal organs extend to the ventral side. Their form and length are of systematic importance for the determina-
215 tion of species. First pair of tentacular cirri very small, often absent (if present, never longer than the tentacles). Second pair of tentacular cirri ("whiskers"), very long, sometimes as long as the body or slightly longer, directed posteriorly; their base is markedly widened. Inner (axial) setae of second pair of tentacular cirri usually with transverse incisions at more or less regular intervals. Parapodia on the body with long stem, ending in 2 pointed branches with leaf-shaped pinnules. The fins form a border on the branches of the parapodia, above and below, and partly cover the stem of the parapodium. Body transparent. Length to 70 mm (one specimen was reported to be 135 mm long).

The genus is divided into two subgenera: Tomopteris s.str. and Johnstonella Gosse; they differ mainly in that the rosette organs and the caudal part with reduced parapodia are absent in Tomopteris s.str. and present in Johnstonella; Tebble (1960) does not think that these characters are sufficient to differentiate the two subgenera, but most authors accept the division of the genus.

Type species: Tomopteris onisciformis Eschscholtz, 1825.

The genus contains about 40 species. Comprehensive keys for the determination of species of Tomopteris were given by Støp-Bowitz (1948) and Dales (1957). The key given below contains only species recorded from the northern regions of the Atlantic and Pacific oceans.

Key to species of the genus Tomopteris Eschscholtz

1 (14). Rosette organs absent (subgenus Tomopteris s.str. Eschscholtz).

2 (5). Caudal appendage sometimes present; hyaline glands present on both fins.

3 (4). Fins with light central and dark marginal parts; the caudal appendage may be long . . . . T. s.str. **nisseni** Rosa, 1908

Wesenberg-Lund, 1935 : 6–9, figs. 13–15; Støp-Bowitz, 1948 : 44–46,

figs. 29–30; Dales, 1957 : 141–142, fig. 52, d (synonymy); Tebble, 1962 : 384–385.
Atlantic, Indian and Pacific oceans (subtropical regions of Japan and coast of California)

4 (3). Fins not divided into dark and light parts; caudal appendage short. . . . . T. s.str. **krampi** Wesenberg-Lund, 1936
Wesenberg-Lund, 1936 : 8–11, figs.1–3; Støp-Bowitz, 1948 : 48–49, figs. 34–35; Dales, 1957 : 142, figs. 51, d, 52, e.
North Atlantic, in the Pacific Ocean off the coast of California

5 (2). Caudal appendage absent.

6 (9). Hyaline glands on ventral fins absent.

7 (8). Hyaline glands present on dorsal fins of 3rd and 4th parapodia . . . . 2. **T.** s.str. **elegans** Chun

216 8 (7). Hyaline glands on dorsal fins absent . . . . ★ T. s.str. **cavallii** Rosa, 1907
Støp-Bowitz, 1948 : 46, figs. 31 – 32; Wesenberg-Lund, 1951 : 33.
North Atlantic (to Davis Strait), Indian Ocean

9 (6). Hyaline glands present only on ventral fins.

10 (11). Chromophile glands small, situated apically . . . . 1. T. s.str. **septentrionalis** Quatrefages

11 (10). Chromophile glands situated ventrally, large.

12 (13). Pinnules forming a border on the stem of the parapodia dorsally and ventrally. ★**T.** s.str. **ligulata** Rosa, 1908
Støp-Bowitz, 1948 : 52, fig. 38; Tebble, 1962 : 384. Subtropical and tropical regions of the Atlantic and Pacific

13 (12). Fins not forming a border on the stem of the parapodia . . . . ★T. s.str. **planctonis** Apstein, 1900
Støp-Bowitz, 1948 : 52–54, figs. 39–40; Wesenberg-Lund, 1950a : 43–44; Tebble, 1962 : 383–384.
Widely distributed (to 45° N in the Northwest Pacific)

14 (1). Rosette organs present (subgenus Johnstonella Gosse).

15 (16). Body ending in a long, thin, threadlike appendage . . . . 3. T. **(Johnstonella) pacifica** Izuka

16 (15). Thin, threadlike appendage at end of body absent.

17 (18). Rosette organs present on stem of 1st and 2nd parapodia . . . .★**T. (Johnstonella) apsteini** Rosa, 1908
Støp-Bowitz, 1948 : 39–42, figs. 26–27; Dales, 1957 : 139, Tebble, 1962 : 385.
Subtropical and tropical regions of Atlantic, Indian and Pacific oceans

18 (17). Rosette organs present on ventral branches of 1st and 2nd parapodia . . . . 4. **T. (Johnstonella) helgolandica** Greeff

Subgenus TOMOPTERIS s.str. Eschscholtz, 1825

Rosette organs absent; hyaline glands usually present. Caudal part with reduced parapodia usually absent. Genital products mainly in dorsal branches of parapodia.

1. **Tomopteris** (s.str.) **septentrionalis** Quatrefages, 1865
(Plate XXIX, Figures 4, 5)

Greeff, 1879 : 276–277, pl. XV, figs. 42, 48, 51 (T. eschscholtzii); Apstein, 1900 : 41, pl. XI, figs. 16–17; Reibisch, 1905 : 9; Izuka, 1914 : 13; Fauvel, 1923 : 224, fig. 84, d; Berkeley, 1924 : 5; Augener, 1929 : 301–302; Benham, 1929 : 195; Monro, 1930 : 86–87; 1936 : 121–122; Wesenberg-Lund, 1935 : 12, pl. I, figs. 7–9, textfig. 2; 1936 : 4–7; Treadwell, 1943 : 39; Støp-Bowitz, 1948 : 49–51, figs. 36–37; Berkeley and Berkeley, 1948 : 26–27, fig. 33; Wesenberg-Lund, 1950a : 43, map 11; 1950b : 12–13; Ushakov, 1955a : 110, fig. 13, D, E; Dales, 1957 : 145, figs. 51, f, 52, g, 54; Tebble, 1960 : 176–177, fig. 8, a, b, figs. 32–33; Imajima, 1961 : 9; Tebble, 1962 : 382–383, fig. 5, Pettibone, 1963 : 97–98, fig. 25, c.

Nuchal organs (epaulets) large, oblong, extending far posteriorly, beyond the eyes. First pair of tentacular cirri always absent. Second pair ("whiskers") 217 slightly longer than half the body. Axial setae of second pair of tentacular cirri with distinct transverse incisions at relatively regular intervals (Figure 7, *10*). Parapodia with conical, pointed branches diverging in different directions. Fins, especially the ventral fins, rounded. Glands absent on dorsal fins. Chromophile glands in the form of diffusely arranged ducts, situated at the apical end of the ventral fins, from the 3rd or 4th pair of parapodia onward; a number of gland cells are also scattered on the ventral fins, which stain with hematoxylin (like the chromophile glands). Rosette organs absent. The small hyaline glands on the ventral fins are situated slightly above the apical chromophile glands; they are usually brownish yellow (these are not rosette organs). First 2 pairs of parapodia usually without glands. Gonads only on dorsal branch of 2nd to 13th or 16th pair of parapodia. Caudal part with reduced parapodia absent, but last pair of parapodia markedly smaller than parapodia on the middle segments. Number of parapodia 20–24. Length to 28 mm, width 8 mm.

Remarks. According to Dales (1955a, 1957), the greatest density of T. septentrionalis near the coast of California (Monterey Bay) was observed in midsummer and midwinter (to 2 specimens per m^3), and Dales therefore assumes that it has a half-yearly cycle of development. According to Wesenberg-Lund (1936), the reproduction period of this species near West Greenland is very prolonged, with a peak in autumn. Numerous larval stages (to 0.2 specimens per m^3) have been recorded in the Kuril-Kamchatka Trench in August, mainly in the surface layers (0–200 m), while the adults concentrate mainly in the 100–750-m horizons in this period (Mileikovskii, 1969).

Distribution. The ZIN collection has specimens from the Norway Sea, the Northwest Pacific and various regions of the southern hemisphere (material of the "Ob" expedition) — about 150 specimens; according to Mileikovskii (1962), it occurs in the Barents Sea. Widely distributed, mainly in cold waters. It occurs in the North Pacific from the Bering Sea to the coast of

California and the east coast of Japan (30° N); recorded from the coast of Chile. Reported from the northern and southern regions of the Atlantic Ocean; north to Baffin Bay.

2. **Tomopteris** (s.str.) **elegans** Chun, 1888 (Plate XXIX, Figures 1–3)

Izuka, 1914 : 12–13; Benham, 1929 : 196–197, pl. II, figs. 24–26; Støp-Bowitz, 1948 : 46–48, figs. 32–33; Ushakov, 1955a : 110; Dales, 1957 : 142, 143, figs. 51, a, 52, a, 53; Tebble, 1960 : 179–180, fig. 11, a–c, fig. 48; 1962 : 380–382, fig, 4, b.

Occipital (nuchal) organs short (ending at border of eye depression). First pair of tentacular cirri always present in juveniles and adults; they are situated immediately behind the cephalic tentacles, which are much shorter and thinner than these (about 2/3 as long). Second pair of tentacular 218 cirri about 2/3 as long as the body. Axial setae of second pair of tentacular cirri with distinct transverse incisions at relatively regular intervals. Parapodia with conical, pointed branches. Chromophile glands, beginning from the 4th pair of parapodia, very large, distinct, situated on the underside of the ventral fins at the end of the branch of the parapodium. Hyaline glands only present on dorsal fins of 3rd and 4th pairs of parapodia, not always distinct. Rosette organs absent. Gonads present only on dorsal branch of parapodia of 3rd–8th body segments. Posterior end without caudal appendage, with reduced parapodia. Number of segments 13–15. Measurements of mature specimens: length 5–8 mm, width including the parapodia 4 mm.

Distribution. The ZIN collection contains 7 specimens from the Northwest Pacific east of Honshu: 34°02' N, 148°44' E and 39°44' N, 151°53' E, horizons 0–50 m. Recorded also from the North Pacific mainly from subtropical and tropical regions. Not found north of the Azores in the Atlantic Ocean. Recorded from the Mediterranean, region of New Zealand and coast of Chile.

Subgenus JOHNSTONELLA Gosse, 1853

Rosette organs present. Hyaline glands absent. Caudal appendage with reduced parapodia. Genital products present in dorsal and ventral branches of parapodia.

3. **Tomopteris (Johnstonella) pacifica** Izuka, 1914 (Plate XXX)

Izuka, 1914 : 11–12, figs. 1–4; Berkeley, 1924 : 289–290, pl. I, figs. 1–2 (T. elegans, preoccupied); 1930 : 75–76 (T. renata); Berkeley and Berkeley, 1948 : 26, figs. 31–32 (T. renata); Ushakov, 1952 : 106–109, figs. 3–5 (T. renata); 1955a : 110, figs. 12 and 13, A–C (T. renata); 1957 : 285–286, map 3 (T. renata + T. pacifica); Dales, 1955a : 440; 1957 : 141, figs. 51, e, 52, f; Berkeley and Berkeley, 1957 : 576 (T. renata); 1960 : 791 (T. renata); Tebble, 1962 : 385–387, fig. 6.

Nuchal organs long; they branch across the line of the eye depression toward the depression. First pair of tentacular cirri (which may be absent in large

specimens) situated on the ventral side, slightly ventral to the cephalic tentacles ("frontal horns"). Second pair of tentacular cirri almost as long as the body. Axial setae of this pair with inner longitudinal striation and indistinct, thin, transverse incisions (Figure 7, *10*). Parapodia with thick stem, ending in 2 short, pointed branches of about the same length. Ends of both branches directed inward and contiguous. The fins of the branches of the parapodia begin on the stem, their margin slightly undulate. Glandular formations distinct without staining. Rosette organs present on the stem of the parapodia on the 2 anterior parapodial segments, at the base of the podial branches, on the inner side on the following segments. Chromophile glands on ventral fins very large and compact, bean-shaped, formed by large,
219 oblong gland cells. Gonads present in dorsal and ventral branches. Caudal part distinctly differentiated as a long, threadlike appendage nearly as long as the body. End of tail slightly swollen (like a bulb), dark reddish brown. Caudal appendage consisting of 12 rudimentary segments. Body semitransparent. Number of parapodia on the body 21–25. Length without caudal appendage to 37 mm, width including the parapodia to 14 mm.

Remarks. The differentiated caudal appendage is characteristic for this species. A similar caudal appendage is present in Tomopteris eura Chamberlin, 1919, which has been only incompletely described. T. eura Chamberlin and T. pacifica Izuka are possibly different names for the same species. In any case, T. eura Chamberlin from the North Pacific is certainly T. pacifica Izuka according to Treadwell (1943). Tebble (1962) reported the largest recorded specimen of Tomopteris — 135 mm long, provisionally determined by him as T. pacifica Izuka.

Distribution. The ZIN collection has 21 specimens from the Sea of Okhotsk and the Bering Sea and adjacent regions of the Pacific (mainly abyssal collections). It occurs only in the North Pacific, north of 40° N; apparently an abyssal species.

4. **Tomopteris (Johnstonella) helgolandica** Greeff, 1879 (Plate XXXI)

Apstein, 1900: 38–39, pl. X, figs. 1–6; Fauvel, 1923: 221–222, fig. 83, h–i; Wesenberg-Lund, 1935: 5–6, figs. 4–6; Støp-Bowitz, 1948: 42–43, fig. 28 (synonymy); Pettibone, 1963: 95–97, figs. 24, 25, a–b.

Nuchal organs oblong. First pair of tentacular cirri absent. Second pair 2/3 as long as the body. Axial setae of second pair of tentacular cirri with slight transverse incisions. Parapodia with long stem and pointed branches of the same length. Fins broad, with slightly undulate margin, completely surrounding the parapodial branches and slightly extending to the stem. Yellowish brown rosette organs near the distal end of the parapodial branches on the inner side of all fins. Rosette organs present on the ventral parapodial branches on the 2 anterior segments. Chromophile glands present on all ventral fins, relatively large. Gonads present in dorsal and ventral parapodial branches. Caudal part present, but not sharply differentiated (without distinct border, as in T. pacifica). Body tapering posteriorly and passing gradually into the caudal part, which has a small podial process with fins at its beginning. Caudal part not longer than 1/3 of the body, with 10–14 rudimentary segments. Body semitransparent, slightly yellowish. One specimen had a punctate pigmented median line on the dorsal side and microscopic punctation on the parapodia. There are 17–20 well developed body segments. Length including the caudal part to 40 mm, width without the parapodia to 3 mm, including the parapodia 12 mm.

220 Remarks. The presence of gonads in the 1st–13th segments has been recorded (Fauvel, 1923; Støp-Bowitz, 1948), but our 2 specimens from the Atlantic Ocean had gonads even in the 17th segment; this has probably no systematic importance and depends on the degree of maturity.

Distribution. The ZIN collection contains 5 specimens from the North Atlantic and the Barents Sea. Widely distributed in the North Atlantic; it occurs in the Mediterranean, off the coast of England; North Sea, north of Iceland, Gulf of Maine and Newfoundland region.

IV. Family Typhloscolecidae Uljanin, 1878

Body transparent, cylindrical, spindle-shaped, tapering toward both ends. Cephalic lobe not sharply separated from 1st segment, conical, ending in a single, elongate, threadlike appendage, the palpod. Two occipital (nuchal) organs in the form of lateral processes ("lateral tentacles") on the cephalic lobe; there is also a median papilla in some forms (sometimes named caruncle). Eyes absent. Pharynx short, with a retort-shaped organ which contains numerous gland cells; this organ is partly everted with the pharynx (piston arrangement). The 2 or 3 anterior segments each have a pair of leaf-shaped cirri (tentacular cirri) which cover the cephalic lobe laterally. Following segments with broad, leaf-shaped dorsal and ventral cirri of about the same size. Cirri with characteristic reticulate structure with numerous gland cells. Podial lobe markedly reduced, very small, with one aciculum and 2, rarely 3 simple, needle-shaped, smooth, setae; setae absent on the anterior segments. Two anal cirri. Length 5–15 mm (maximum length 35–40 mm).

An aberrant group of pelagic polychaetes, characterized by the reduction of the podial lobe, the almost total absence of setae, and transformation of the dorsal and ventral podial cirri into large leaf-shaped appendages which function as rowing organs. Dorsal and ventral cirri easily lost after fixation, so that most fixed specimens have no appendages.

The family contains only 3 genera: Typhloscolex Busch, Travisiopsis Levinsen and Sagitella Wagner. The status of the genus Typhlodrilus Baldasseroni, 1909 is doubtful, and Friedrich (1950) considers is as a synonym of Typhloscolex Busch. The genera differ mainly in the form and structure of the anterior end. The most detailed study of the species of Typhloscolecidae is by Friedrich. The systematic position of this family is not quite clear. Dales (1955) considers the Typhloscolecidae as neotenic forms which developed from pelagic Phyllodocidae.

Key to genera of the family Typhloscolecidae

1 (2). Cephalic lobe with margins of ciliary ridges dorsally and ventrally. . . . . 1. **Typhloscolex** Busch (p. 209)
2 (1). Cephalic lobe without ciliary ridges at the margins.
221 3 (4). Median papilla present . . . . 2. **Travisiopsis** Levinsen (p. 210)
4 (3). Median papilla absent . . . . 3. **Sagitella** Wagner (p. 212)

1. Genus **TYPHLOSCOLEX** Busch, 1851

Body slender, cylindrical, semitransparent, slightly wider anteriorly, tapering posteriorly. Cephalic lobe ending in a single median tentacle with a thick base (palpod), and with dorsal and ventral ridges which form a broad fringe. Margin of ridges with long cilia which function as a rotatory apparatus, resembling that of Rotatoria to some extent. Two small lateral processes beneath the dorsal ridge (nuchal organs). First 3 anterior segments with a pair of broadly leaf-shaped cirri (tentacular cirri); all following segments with 2 pairs of cirri of about the same size (dorsal and ventral cirri). Two long anal cirri. Podial lobe with a small aciculum and 1–3 small, little projecting setae (mainly on the posterior segments).

Small worms, less than 15 mm long, floating in the water in a vertical position.

Type species: Typhloscolex muelleri Busch, 1851.

Several species have been described, which differ mainly in the form of the ciliary ridges and position of the nuchal organs (Støp-Bowitz, 1948; Friedrich, 1950). However, the ciliary ridges change markedly after fixation, so that this is not a reliable character for the differentiation of species. The most common, widely distributed species is Typhloscolex muelleri Busch.

1. **Typhloscolex muelleri** Busch, 1851 (Plate XXXII, Figures 1–5)

Reibisch, 1895: 52–53, pl. V, figs. 1–5; Ehlers, 1913: 530; Fauvel, 1923: 226–227, fig. 85, f–h; Augener, 1929: 307–308; Monro, 1930a: 90; Yashnov, 1940: 58; Treadwell, 1943: 38, fig. 27; Støp-Bowitz, 1948: 55; 1949: 17–18, fig. 8; Berkeley and Berkeley, 1948: 30, fig. 39; Ushakov, 1952: 110; 1955a: 112, fig. 14, A–C; 1957: 286, map 4; Dales, 1957: 146–147, fig. 55, a–b; Tebble, 1960: 195–196, 231–236, figs. 34–36, tables 16, 17; Imajima, 1961: 7, fig. 2; Tebble, 1962: 408–409.

Dorsal and ventral ciliary ridges on cephalic lobe very large, forming a wide fringe which is almost as high as the width of the cephalic lobe. Cilia long, forming a dense brush. Under the dorsal ridge are 2 distinct lateral processes, the nuchal organs. First pair of tentacular cirri, which cover the sides of the cephalic lobe, with a small median incision (bilobed). Dorsal and ventral podial cirri rounded, slightly oblong. Setae sometimes present from the 5th segment onward (i.e. from the 2nd segment with dorsal and ventral cirri), but setae usually present only on the posterior segments. Two, rarely 3, setae on each podial lobe. Setae needle-shaped, projecting only little beyond the podial lobe. Anal cirri oblong-oval, larger than the posterior podial cirri. Body grayish white, semitransparent. Number of segments 25–35. Length 5 mm, rarely 10–15 mm.

222 Distribution. The ZIN collection has specimens from the Norway Sea, southwestern part of the Barents Sea, central regions of the Polar Basin, Sea of Okhotsk and Bering Sea, Northwest Pacific, and, in the material of the "Ob" expedition, 1956–1958, various regions in the southern hemisphere (over 250 specimens). Widely distributed, common in the North Pacific.

2. Genus **TRAVISIOPSIS** Levinsen, 1885 (emend. Tebble, 1962)

(Plotobia Chamberlin, 1919)

Body cylindrical, spindle-shaped. Cephalic lobe conical, pointed, ending in a finger-shaped process (palpod). On the dorsal side of the posterior part of the cephalic lobe is a large median papilla (sometimes not distinct, or absent – in Tr. dubia). Two nuchal organs surrounding the median papilla anteriorly and then continuing as two free, elongate processes. One pair of leaf-shaped tentacular cirri on the 3 anterior segments which cover the cephalic lobe laterally. Dorsal and ventral leaf-shaped cirri of about the same size on the following segments. Two broad anal cirri. One to 3 setae of acicular type, small, mainly on the posterior segments.

Type species: Travisiopsis lobifera Levinsen, 1885.

The genus contains 6 species; Travisiopsis capensis McIntosh, 1924, recorded from South Africa, is a species incertae sedis.

Key to species of the genus Travisiopsis Levinsen

1 (10). Median papilla large, distinct.
2 (3). Nuchal organs divided . . . . * **Tr. coniceps** (Chamberlin)
Chamberlin, 1919a: 156–157, pl. 66, figs. 2–4 (Plotobia); Støp-Bowitz, 1948: 61; Dales, 1957: 150.
Southern Atlantic Ocean, littoral of Peru and San Francisco region (Monterey Bay) in the Pacific
3 (2). Nuchal organs not divided.
4 (5). Nuchal organs without lateral processes behind the median papilla . . . . * **Tr. lumbricoides** Reibisch
Reibisch, 1895: 57, pl. V, figs. 10–12.
Atlantic Ocean (Sargasso Sea)
5 (4). Nuchal organs with lateral processes behind the median papilla.
6 (7). Lateral processes of nuchal organs long, reaching to the 4th segment; median papilla with a posterior finger-shaped process. . . . . 3. **Tr. lanceolata** Southern
7 (6). Lateral processes of nuchal organs short; median papilla rounded or rectangular (without posterior finger-shaped process).
8 (9). Lateral processes of nuchal organs parallel; 21 segments. . . . . 1. **Tr. lobifera** Levinsen
9 (8). Lateral processes of nuchal organs directed laterally; 25 segments . . . . 2. **Tr. levinseni** Southern
223 10 (1). Median papilla absent or indistinct . . . . . * **Tr. dubia** Støp-Bowitz
Støp-Bowitz, 1948: 60–61, fig. 48; Tebble, 1962: 414–415, fig. 20.
Atlantic Ocean (40–48° N), Strait of Malacca, subtropical regions of the North Pacific

1. **Travisiopsis lobifera** Levinsen, 1885 (Plate XXXII, Figure 7, Plate XXXIII, Figures 1–4)

Levinsen, 1885 : 336–340, pl. I, figs. 17–20; Reibisch, 1895 : 95; Fauvel, 1923 : 229, fig. 86, a–d; 1932 : 66–67; Støp-Bowitz, 1948 : 57–58, fig. 44; Ushakov, 1957 : 286–287, fig. 7, d–g; Berkeley and Berkeley, 1957 : 577–578; Dales, 1957 : 148–150, figs. 58–60 (part); Tebble, 1960 : 196–197, 245, figs. 13, a, 45; 1962 : 411, fig. 19.

Median papilla rounded, slightly transverse-oval. Nuchal organs partly surrounding median papilla anteriorly and forming two short parallel processes behind it. Cephalic lobe covered laterally by 3 pairs of tentacular cirri, corresponding to the first 3 circumoral segments. Tentacular cirri broad, concave, spoon-shaped. Dorsal and ventral podial cirri broad, irregularly heart-shaped on the following segments. Podial lobe with an aciculum and 1–3 small setae (from the 5th segment onward). Anal cirri very large, broad, rectangular with slightly rounded corners. Coloration of fixed specimens yellowish gray. Number of segments 21. Length 5–10 mm, width 1 mm (length to 25 mm according to the literature).

Distribution. In the ZIN collection are 2 specimens from the Northwest Pacific and 5 specimens from the southern hemisphere (Tebble, 1968). According to the literature, it is widely distributed in the southern and northern Atlantic Ocean; northern boundary of distribution in the Pacific mainly that of subtropical waters (Tebble, 1962).

2. **Travisiopsis levinseni** Southern, 1910 (Plate XXXII, Figures 8–11)

Southern, 1910b : 429; 1911 : 32–33, pl. II, figs. 7–10; ?Ehlers, 1913 : 520, pl. XXXIX, figs. 16–17 (Sagitella opaca); Fauvel, 1923 : 229–230, fig. 86, h–k; Benham, 1927 : 80–81, pl. II, figs. 33–34 (Sagitella kowalewskii); Monro, 1930 : 89–90 (Sagitella kowalewskii); Wesenberg-Lund, 1935 : 13–14; 1936 : 12–16, figs. 4–5; Monro, 1936 : 123–124, fig. 17 (Tr. benhami); Støp-Bowitz, 1948 : 59–60, figs. 46, 47, a–b; Ushakov, 1955a : 114, fig. 14, d–g; 1957 : 288, map 4; Dales, 1957 : 150; Tebble, 1960 : 197–198, 236–237, figs. 13, b, 36; 1962 : 412–413.

Median papilla rectangular, slightly wider posteriorly. The nuchal organs form two short semicircular processes directed laterally behind the median papilla; before and slightly lateral to the median papilla are two round caruncules, which according to Wesenberg-Lund (1936) are part of the same formation as the nuchal processes. Cephalic lobe covered laterally by 3 pairs of large, spoon-shaped tentacular cirri; tentacular cirri directed
224 straight anteriorly. Dorsal and ventral cirri of anterior segments slightly pointed, almost square, with a broad base on the middle segments, and dorsal cirri on the posterior segments elongate, pointed, much longer than the ventral cirri. Podial lobe small, indistinct. Small setae of acicular type present from the 6th segment or farther on, 2 or 3 on each parapodium. Anal cirri broadly spatulate, larger than the dorsal cirri on the posterior segments. Fixed specimens yellowish pink. Number of segments 25. Length to 20 mm, width 2 mm (Tebble states that they may be 35 mm long).

Distribution. The ZIN collection has one specimen from the Kuril Islands ("Vityaz," 1949, station 166, depth 0–4000 m) and 54 specimens from various regions in the southern hemisphere (Tebble, 1968). Widely distributed, to Davis Strait (1130–3500 m) in the North Atlantic; recorded from the North Pacific, apparently from abyssal horizons (Tebble, 1962).

3. **Travisiopsis lanceolata** Southern, 1910 (Plate XXXII, Figure 6; Plate XXXIII, Figures 5–7)

Southern, 1910b: 428; 1911: 30–32, pl. I, figs. 3, 5, 6; ? Ehlers, 1913: 527–529, pl. XXXIX, figs. 8–14 (Sagitella cornuta); Chamberlin, 1919a: 155–156, pl. 65, figs. 6–11, pl. 66, fig. 1 (Plotobia simplex); Fauvel, 1923: 229, fig. 86, e–g; Wesenberg-Lund, 1935: 13; 1939: 20–21, fig. 16; Treadwell, 1943: 38 (Plotobia simplex); Støp-Bowitz, 1948: 58–59, figs. 45–46; Wesenberg-Lund, 1950: 44; Dales, 1957: 148–150, figs. 58–60 (Tr. lobifera, part); Tebble, 1960: 198–199, 246, figs. 13, c, 45; 1962: 413.

Median papilla T-shaped, with long, narrow posterior end. Nuchal organs partly surrounding the median papilla anteriorly; their long posterior processes extend to the 4th segment. Dorsal and ventral podial cirri, at first square, then oblong. Anal cirri spatula-shaped. Number of segments 22. Length to 38 mm.

Distribution. The ZIN collection contains one specimen from the South Pacific, Easter Island region, 37°55' S, 109°24' W (Tebble, 1968). According to the literature, found in the Atlantic Ocean from the southern subtropical convergence to 60° N, in the North Pacific to 50° N.

3. Genus **SAGITELLA** N. Wagner, 1872

Body cylindrical, spindle-shaped, elongate. Cephalic lobe conical, ending in an elongate, threadlike appendage (palpod). Two nuchal organs on the cephalic lobe (some authors name these organs lateral tentacles). Median papilla (caruncle) absent, only a slight thickening on the dorsal side of the cephalic lobe. One pair of tentacular cirri on each of the 3 anterior segments; following segments with dorsal and ventral cirri. All cirri broadly leaf-shaped. Two large anal cirri. Podial lobes small, with an aciculum and 1–3 small, needle-shaped setae which project slightly outward.

Type species: Sagitella kowalewskii N. Wagner, 1872.

225 Monotypic genus. S. barbata and S. praecox, described by Uljanin (1878), belong to the genus Typhloscolex Busch. The description of S. opaca Ehlers, 1913 is incomplete, but this species does not belong to the genus Sagitella and is possibly a synonym of Travisiopsis levinseni Southern. Two other species described by Ehlers, S. lobilifera Ehlers, 1912 and S. cornuta Ehlers, 1913, also belong to the genus Travisiopsis Levinsen.

1. **Sagitella kowalewskii** Wagner, 1872 (Plate XXXIII, Figures 8–11)

Wagner, 1872: 344–347, fig. (form A); Uljanin, 1878: 1, pl. IV; Reibisch, 1895: 56, pl. 5, fig. 9; Southern, 1911: 33–34, pl. 2, figs. 11–12; Ehlers, 1913: 526, pl. XXXIX, fig. 15; Fauvel, 1923: 128, fig. 85, a–c; Okuda, 1937a: 76–77, fig. 2; Treadwell, 1943: 38, pl. II, fig. 26 (*Plotobia paucichaeta*); Støp-Bowitz, 1948: 56–57, fig. 43; Berkeley and Berkeley, 1948: 31, fig. 40; Ushakov, 1952: 109; 1955a: 114, fig. 14, H–I; 1957: 288–289, map 4; Dales, 1957: 147–148, figs. 56, 57, 60; Imajima, 1961: 7–8; Tebble, 1962: 410.

Cephalic lobe conical, with a finger-shaped appendage (palpod) at the distal end and two nuchal organs which form 2 lateral, rounded processes. Tentacular cirri of first 3 segments broadly leaf-shaped. First pair partly covering the cephalic lobe. The following segments with dorsal and ventral, leaf-shaped cirri which are irregularly heart-shaped, all of about the same size. Anal cirri very broad, flattened, nearly square. Parapodia with 2–3 short acicular setae; setae absent on first 4 segments. Coloration yellowish pink. Number of segments to 50. Length to 15 mm.

Mature specimens with ripe eggs were found in the region of the Kuril Islands in October.

Remarks. The incompletely described species *Plotobia paucichaeta* Treadwell (1943: 38–39) closely resembles *Sagitella kowalewskii* Wagner to judge by the drawing of the cephalic end, and is possibly a synonym of this species.

Distribution. Our collection contains specimens from the Northwest Pacific, region of the Kuril Islands (Ushakov, 1957), and from the region of Easter Island, the Southeast Pacific (Soviet Antarctic Expedition ("Ob"), 1956–1958) and from tropical regions of the Indian Ocean (Tebble, 1968). Widely distributed, mainly in tropical and subtropical regions.

V. Family Lacydoniidae Bergström, 1914

(Paralacydoniidae Pettibone, 1963)

Body thin, long, consisting of a small number of body segments of the same type. Cephalic lobe rounded or oblong (conical). Four cephalic tentacles at anterior end of cephalic lobe. First (circumoral) segment without appendages or setae, or only with a pair of very small tentacular cirri. Proboscis with soft, marginal (oral) papillae (*Lacydonia*, *Paralacydonia*), or completely covered with numerous threadlike papillae (*Pseudolacydonia*); 226 chitinous jaws absent; proventriculus muscular. Parapodia biramous on all segments, or uniramous only on the 1st–3rd anterior segments. Dorsal and ventral cirri relatively small, papilliform or leaf-shaped; branchial processes absent. Dorsal ramus of parapodia with long, simple setae, ventral ramus with segmented setae. Benthic species.

The family contains only 3 genera: *Lacydonia* Marion and Bobretzky, 1875, *Paralacydonia* Fauvel, 1913 and *Pseudolacydonia* Rullier, 1964, with only a few species.

Bergström's (1914) statement that the Lacydoniidae have chitinous jaws has not been confirmed.

Key to genera of the family Lacydoniidae

1 (2). Tentacular cirri present. Parapodia uniramous on the 2–3 anterior setose segments . . . . 1. **Lacydonia** Marion and Bobretzky (p. 214)
2 (1). Tentacular cirri absent.
3 (4). Cephalic tentacles small, two-segmented. Parapodia on 1st setose segment uniramous, on all other segments biramous . . . . 2. **Paralacydonia** Fauvel (p. 215)
4 (3). Cephalic tentacles long, thin. Parapodia of 1st setose segment biramous, as on the other segments . . . . * **Pseudolacydonia** Rullier, 1964
This genus contains only the single species P. caeca Rullier, from the west coast of Africa (Rullier, 1964)

1. Genus **LACYDONIA** Marion and Bobretzky, 1875

Cephalic lobe rounded, cephalic tentacles very small. Proboscis with 10–24 soft marginal papillae. First circumoral segment with a pair of short tentacular cirri; setae absent. Next 2–3 segments with uniramous parapodia, all other segments with biramous parapodia, with distinctly diverging branches. Dorsal and ventral cirri small, papilliform. Dorsal setae simple, slightly curved; ventral setae segmented, heterogomph.

Type species: Lacydonia miranda Marion and Bobretzky, 1875.

The genus contains 4 species; the recently described Lacydonia incognita Rullier, 1965a, from the coast of West Africa, has been placed provisionally in the genus Lacydonia, since the species was described from a fragment without a head. It differs markedly from all other species of Lacydoniidae in the structure of the parapodia; however, its systematic position is not clear. Its relation to the genus Lacydonia seems doubtful, and the parapodia suggest that this species belongs to the genus Paralacydonia; I leave L. incognita Rullier provisionally in the genus Lacydonia until further material becomes available.

Eliason (1962b : 235) recorded 3 specimens of Lacydonia from the Oresund, depth 271–487 m; he considers them as closely related to L. miranda Mar. and Bobr., but these specimens have a distinct single papilla on the cephalic lobe (!); according to this character, the specimens should be considered as belonging to a different genus.

227 Key to species of the genus Lacydonia Marion and Bobretzky

1 (6). Podial lobes not covered anteriorly and posteriorly by leaf-shaped lobes.
2 (5). Eyes present.
3 (4). Eyes large. Parapodia uniramous on the first 3 setose segments . . . . ***L. miranda** Marion and Bobretzky, 1875
Fauvel, 1923 : 198, fig. 74, a–d.
Mediterranean, English Channel, littoral of Ireland
4 (3). Eyes small. Parapodia uniramous only on the first 2 setose seg-

ments . . . . L. mikrops Ehlers
Ehlers, 1913: 459–460, pl. XXIX, figs. 5–10.
Antarctic (Wilhelm II Land)

5 (2). Eyes absent . . . . 1. **L. papillata** Uschakov

6 (1). Podial lobes covered anteriorly and posteriorly by large leaf-shaped lobes . . . . ***L. incognita** Rullier, 1965
Rullier, 1965a: 22–24, fig. 2.
West Africa, littoral of Dahomey

1. **Lacydonia papillata** Uschakov, 1958 (Plate XXXIV, Figures 1–3)

Ushakov, 1958a: 206–207, fig., D–F.

Cephalic lobe broad, semicircular anteriorly; dorsal pair of cephalic tentacles slightly larger than the ventral pair, which is not visible from the dorsal side. Dorsal side of cephalic lobe, behind the tentacles, with 2 large lateral depressions (sensory pits?) outlined by brown pigmentation; similar dark pigmentation at the posterior margin of the cephalic lobe. Eyes absent. Pharynx not examined (retracted). Cephalic lobe distinctly separated from the 1st circumoral segment, which is without setae but with a pair of very small tentacular cirri. Three following segments (2nd–4th) with uniramous parapodia, with one bundle of segmented setae; other segments with biramous parapodia, their rami (dorsal and ventral) widely separated. Dorsal branches of parapodia with thin, simple hairlike setae; ventral branches with segmented setae and very thin, long distal part. Dorsal and ventral cirri rudimentary, papilliform, indistinct. The type showed clearly 4 large, papilliform dark spots on the dorsal side behind the 1st setose segment. Papillae not recognizable on the anal lobe (possibly lost).

Coloration light olive green. Number of segments 33. Length 5.5 mm, width 0.5 mm.

Type deposited at ZIN AN SSSR, No. 1/1622.

Distribution. Kuril-Kamchatka Trench, 41°11' N, 154°56' E, depth 5070 m ("Vityaz," 1953); 2 fragments of anterior part of body collected in 2 stations southeast of Honshu, depths 3352 and 5690 m ("Vityaz," stations 3886 and 3517).

228 2. Genus **PARALACYDONIA** Fauvel, 1913

Cephalic lobe oblong, cephalic tentacles small, two-segmented. Proboscis with 10 soft, marginal papillae. First circumoral segment without tentacular cirri and setae. Parapodia of 2nd segment uniramous, on all following segments biramous, their branches widely separated. Dorsal and ventral cirri small, pointed. Notopodium with simple setae, neuropodium with segmented setae, sometimes also with 1–2 simple setae in the lower part of the bundle.

Type species: Paralacydonia paradoxa Fauvel, 1913.

Only 2 species of this genus have been described: P. paradoxa Fauvel, 1913 and P. weberi Horst, 1923 (= P. mortenseni Augener, 1924), which are probably the same species (see below).

In the general form of the body, the structure of the parapodia, and the form of the pharynx, Paralacydonia resembles juveniles of Nephthys.

Larval stages of Paralacydonia have been described recently by Bhaud (1967); the early trochophore combines the characteristics of the Phyllodocidae and Nephthyidae (see p. 52 and Figure 18).

1. **Paralacydonia paradoxa** Fauvel, 1913 (Plate XXXIX, Figures 4–9)

Fauvel, 1913 : 54–55, fig. 10; 1914 : 118–121, pl. 7, figs. 1–9; 1923 : 198–199, fig. 74, a–d; Ushakov, 1958 : 416–419, fig. 1, A–D; Hartman and Barnard, 1960 : 86–87, pl. 6, figs. 1–3; Hartman, 1963 : 11; Pettibone, 1963 : 184–186, fig. 46; Ushakov and Wu Pao-ling, 1965 : 156–157, fig. 2, E–H; Day, 1967 : 350–351, fig. 15, e–h.

Cephalic lobe oblong (about twice as long as wide). Cephalic tentacles two-segmented. Two longitudinal grooves on the dorsal side of the cephalic lobe. Eyes absent. A small shield (swelling) on the posterior margin of the cephalic lobe which extends over the 3 anterior segments. Proboscis short, smooth, without papillae. Two thick lips at its distal end; on their outer margin are 4 lateral elongate teat-shaped papillae, and an additional short papilla anteriorly and posteriorly. The marginal teat-shaped papillae on the proboscis are sometimes dark brown, sometimes colorless. Proventriculus long, thick and strongly muscular (with circular muscles), with a dark longitudinal cord, and there were small, rounded, thickened areas in transverse rows in one specimen, as in some Syllidae. First segment without parapodia, parapodia not fully developed on the 2nd segment (with one bundle of setae). Parapodia biramous on all following segments, their dorsal and ventral branches widely separated. Anterior lobes of notopodia and neuropodia oblong, with a small incision corresponding to the aciculum; posterior lobes shorter, rounded. Dorsal branch of parapodia slightly shorter than the ventral and with a bundle of simple, short setae. Ventral branch of parapodia with segmented setae, but there are also 1 or 2 simple setae in the lower part of the bundle; these simple setae were not present in all specimens. Ventral setae slightly longer and more numerous than the dorsal setae. Ventral setae heterogomph; distal part very long, finely denticulate. Noto-
229 podia and neuropodia covered with small villi on the inside. Anal lobe barrel-shaped, with 2 long anal cirri. Coloration pale yellowish. Small dark spots are present on the podial processes in some specimens from the Yellow Sea; there are small dark dots on the dorsal and ventral side in some specimens from abyssal stations in the Pacific Ocean. Number of segments to 60. Length to 15 mm, width including the parapodia 1.5 mm (maximum width in anterior part of body, in region of pharynx).

Eggs very large; females have been recorded from the Yellow Sea in July, from the equatorial zone of the Pacific at the end of August.

Remarks. The differences between P. paradoxa Fauvel and P. weberi Horst (= P. mortenseni Augener) are not sufficiently distinct. According to Fauvel (1932), these species differ mainly in that simple setae in the lower part of the neuropodium are absent in P. weberi, but are present in P. paradoxa. Our material contained specimens with simple setae on the neuropodia and specimens without such setae; no correlation between the presence or absence of these setae and the size of specimens, depth or geographical region could be found; one specimen from New Guinea (depth 530 m), i.e. from about the same region from which P. weberi was described, had simple setae on the neuropodium. Simple setae are possibly sometimes overlooked due to bad preservation. These two species are perhaps identical (Ushakov, 1958).

P. paradoxa has recently been recorded from different regions of the oceans; it is a very eurybathic species. Thus, it was found on the coast of California at a depth of over 1750 m (Hartman and Barnard, 1960), on the Atlantic coast of North America at a depth of 105–122 m (Pettibone, 1963), and at depths of less than 100 m in the littoral of South Africa and Mozambique (Day, 1967). We collected it at depths from 7 to 5498 m. Some populations may show differences. Day (1967) stated that African specimens had a pair of indistinct eyes, but eyes were not found by Fauvel in typical specimens from the Mediterranean, nor in our fixed specimens; there may also be differences in the pigmentation.

A new subspecies has been recently described from the coast of Japan, P. paradoxa japonica Kitamori, 1965; it differs from the typical form as follows: the presence of a small depression at the anterior end of the prostomium and of a small median papilla on the pygidium, in addition to 2 long anal cirri.

Distribution. The ZIN collection contains 62 specimens from the Yellow Sea (depth 7–25 m), South China Sea, Gulf of Tonkin (depth 48–130 m), western part of the Pacific, south of 40° N to the equator (depth 250–5498 m). Widely distributed, recorded from the Mediterranean, the coast of Morocco, South Africa, the Atlantic and Pacific coasts of North America; P. weberi was recorded from the coasts of India, Indonesia and the northern part of New Zealand.

PLATES I–XXXIV

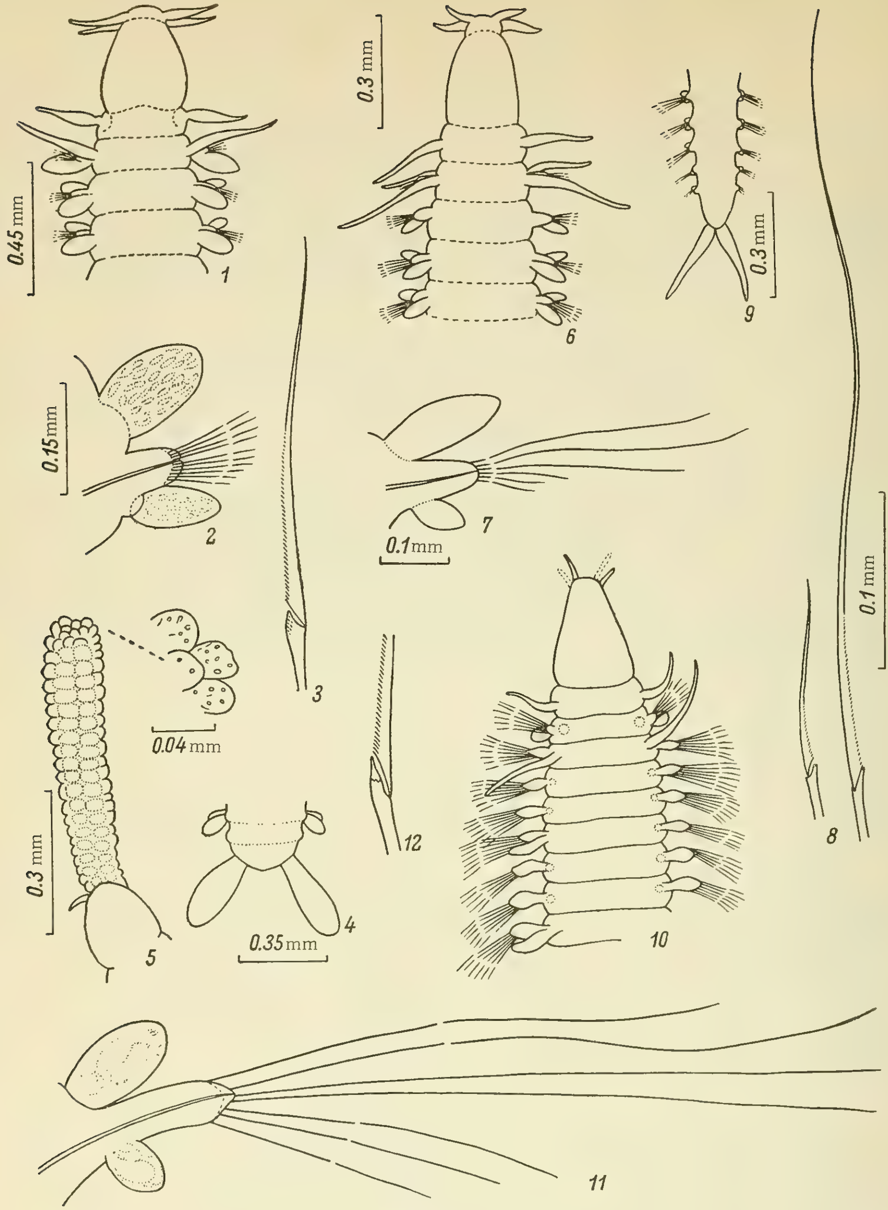

PLATE I

Lugia abyssicola Uschakov: 1) cephalic end, dorsal; 2) parapodium from middle of body; 3) seta with long distal part; 4) pygidium (southeast of Hokkaido, type); 5) partly everted proboscis and papillae on proboscis (paratype).

Mystides schroderae Uschakov: 6) cephalic end, dorsal; 7) parapodium from middle of body; 8) setae with short and long distal part; 9) posterior end with anal cirri (Hawaiian Islands, type).

Protomystides levensteinae Uschakov: 10) cephalic end, dorsal; 11) parapodium from middle of body; 12) seta (Mariana Islands, type).

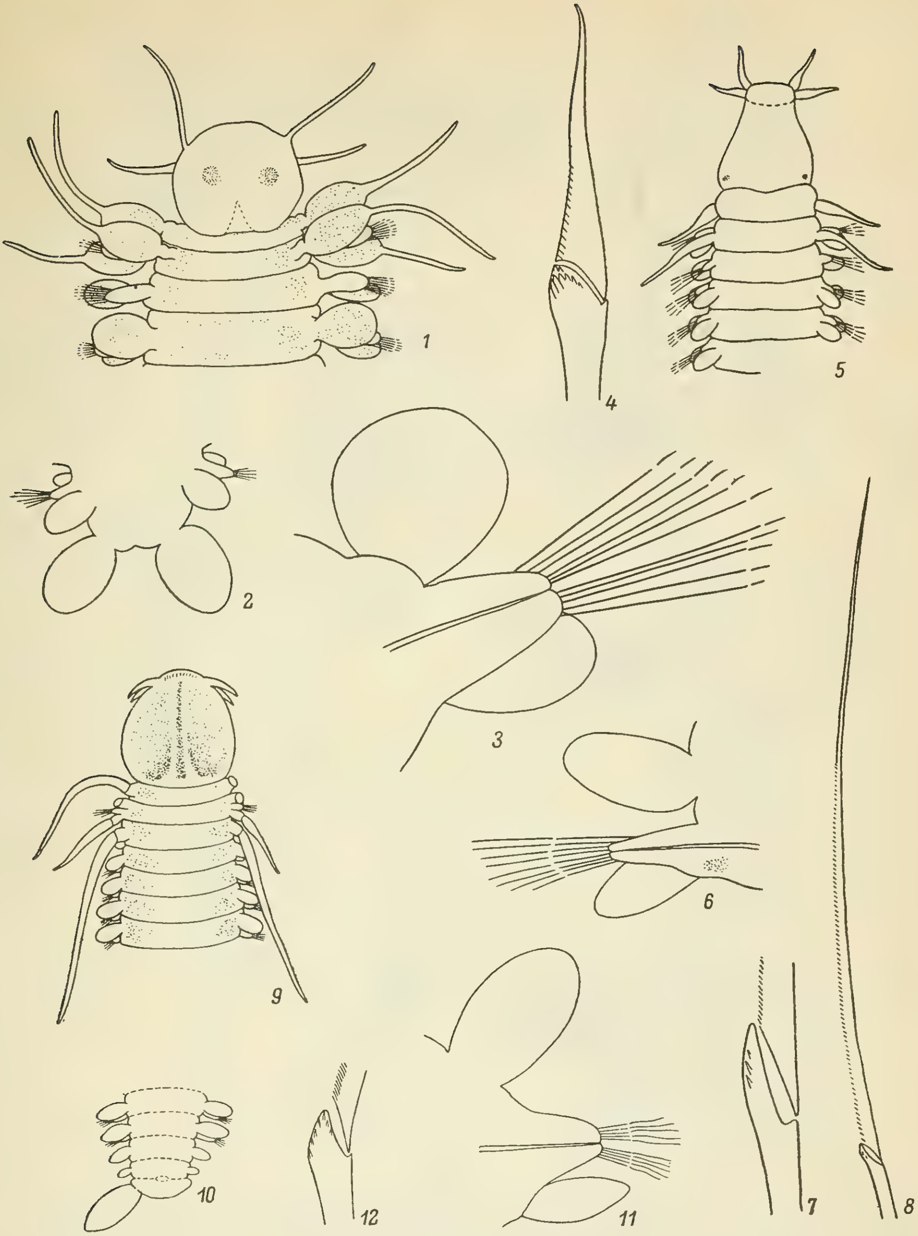

PLATE II

Mystides borealis Théel: 1) cephalic end, dorsal; 2) pygidium with anal cirri; 3) parapodium from middle of body; 4) seta (Kuril Islands).

Mystides rarica (Uschakov): 5) cephalic end, dorsal; 6) parapodium from middle of body; 7) articulation of seta; 8) seta (Kuril - Kamchatka Trench).

Protomystides orientalis Uschakov: 9) cephalic end, dorsal; 10) posterior end, dorsal; 11) parapodium from middle of body; 12) seta (east of Honshu, type).

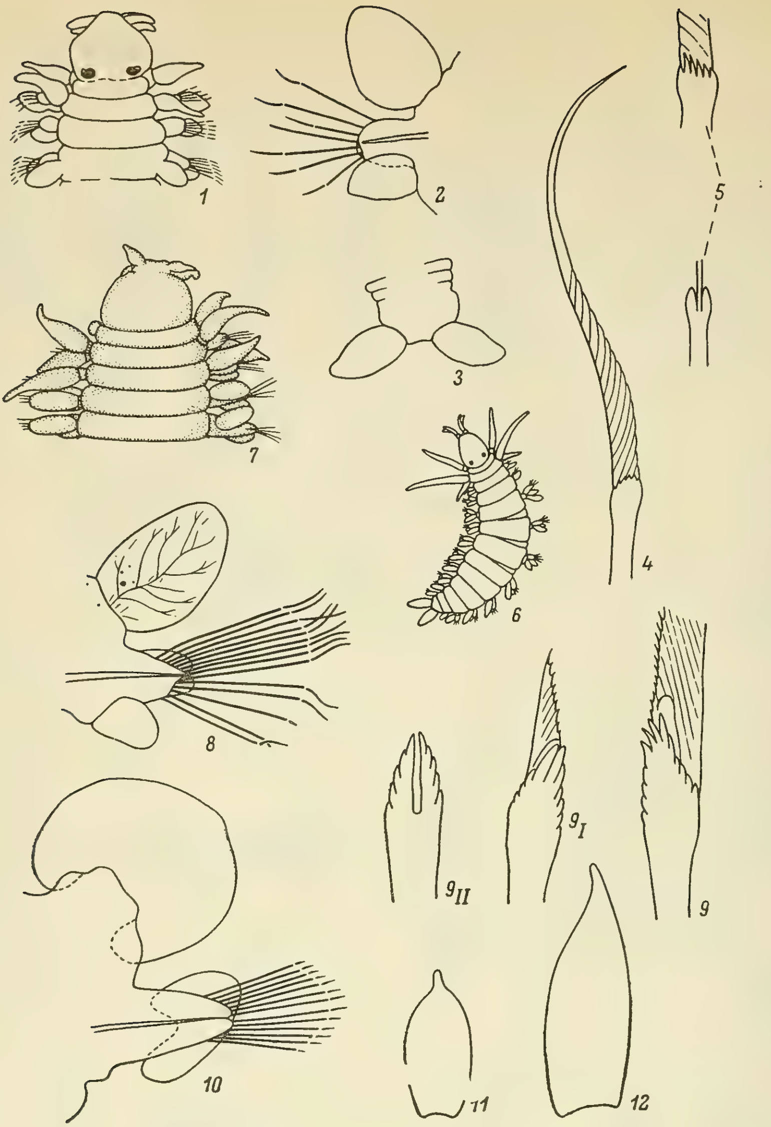

PLATE III

Mystides southerni Banse: 1) cephalic end; 2) parapodium from middle of body; 3) pygidium; 4) seta; 5) articulation of seta, frontal and lateral (after Banse, 1954); 6) general view (after Sveshnikov, 1958).
Protomystides occidentalis (Ditlevsen): 7) cephalic end; 8) parapodium from middle of body; 9) setae with long and short distal part (after Hartmann-Schröder, 1963).
Genetyllis lutea Malmgren: 10) parapodium of 30th segment; 11) cephalic tentacle; 12) ventral tentacular cirrus of 2nd segment (Kattegat).

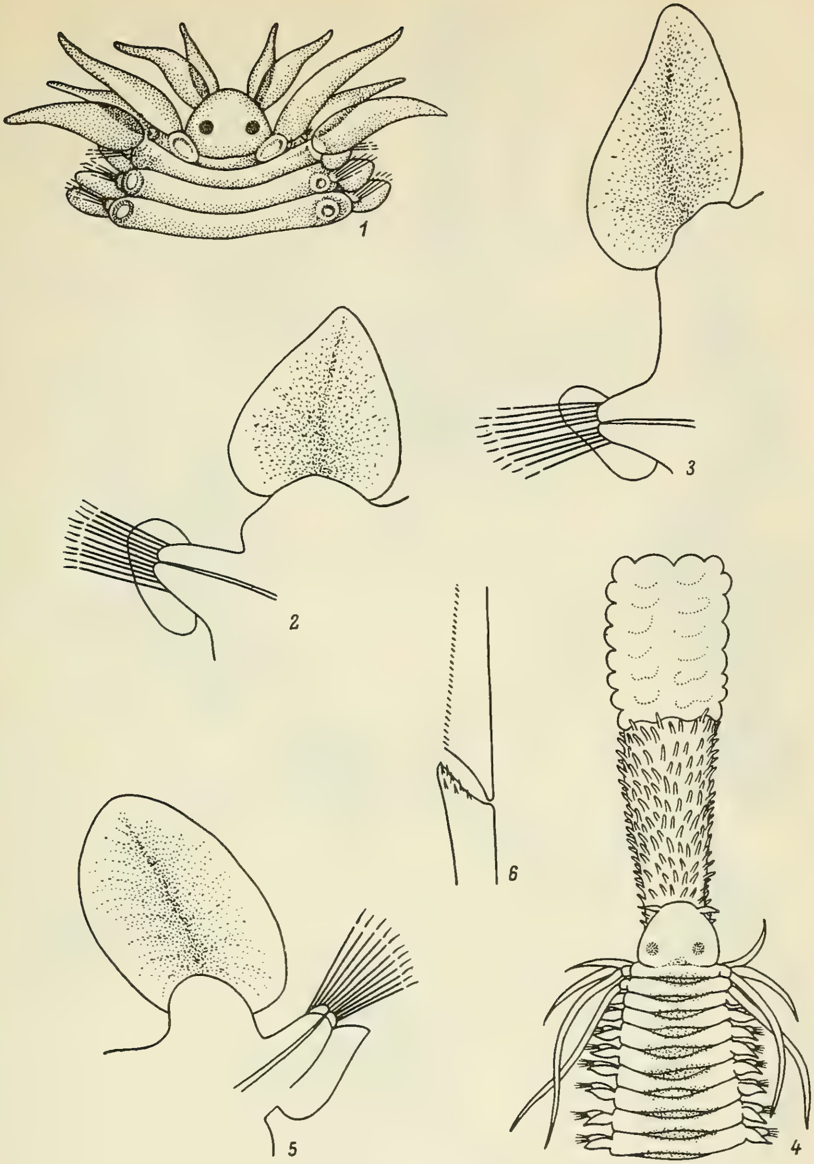

PLATE IV

Genetyllis castanea (Marenzeller): 1) cephalic end, dorsal tentacular cirri of 2nd segment not shown (Sea of Japan); 2) parapodium from middle of body (Hainan); 3) same (Sea of Japan).
Phyllodoce malmgreni Gravier: 4) cephalic end with everted pharynx; 5) parapodium from middle of body; 6) seta (Red Sea).

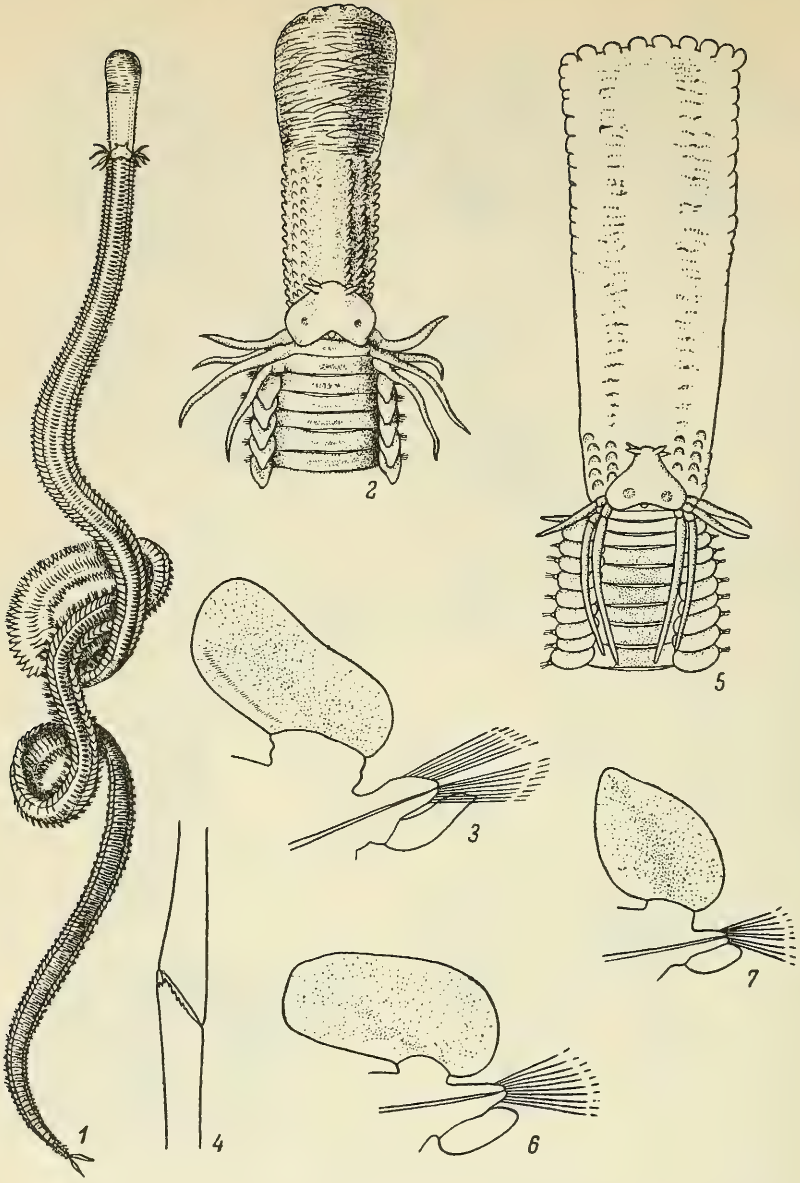

PLATE V

Phyllodoce (Anaitides) groenlandica Oersted: 1) general view (×2); 2) cephalic end, dorsal, with everted pharynx; 3) parapodium from middle of body; 4) seta (Sea of Japan).

Phyllodoce (Anaitides) citrina Malmgren: 5) cephalic end, dorsal, with everted pharynx; 6) parapodium from middle of body (Sea of Okhotsk).

Phyllodoce (Anaitides) maculata (L.): 7) parapodium from middle of body (Kuril Islands).

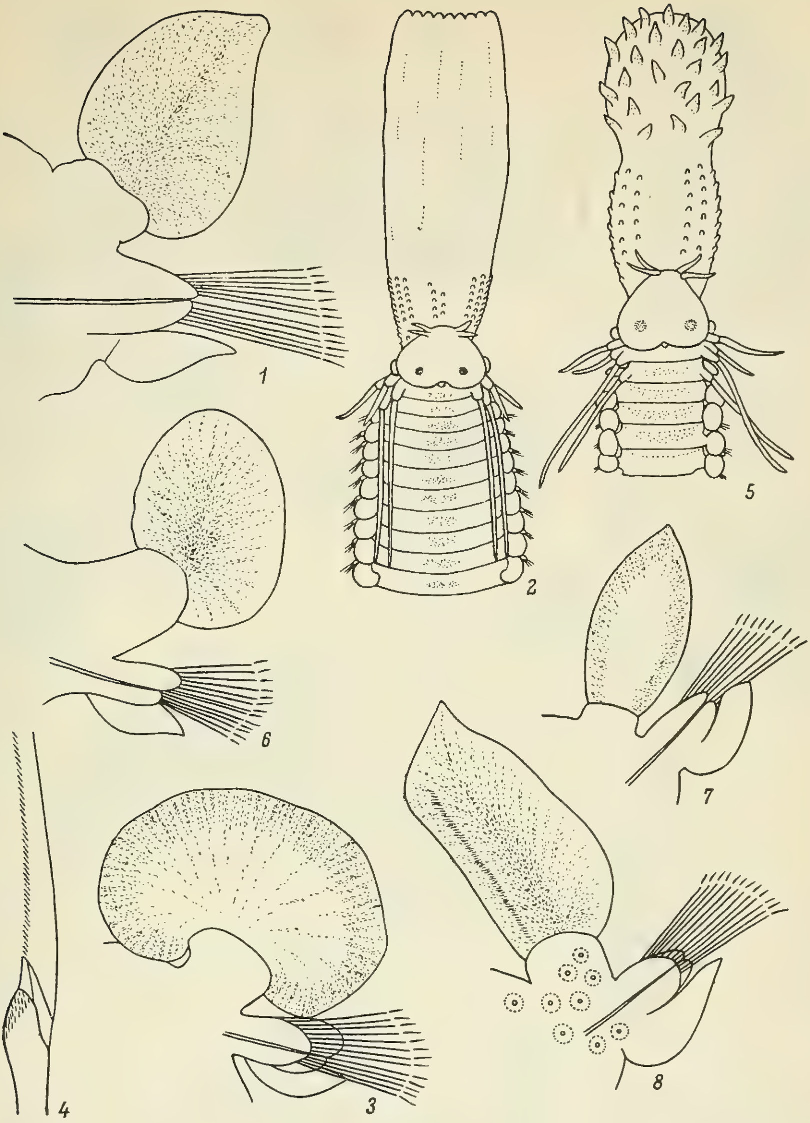

PLATE VI

Phyllodoce (Anaitides) mucosa Oersted: 1) parapodium from middle of body (Black Sea).
Phyllodoce (Anaitides) chinensis Uschakov and Wu: 2) cephalic end, dorsal, with everted pharynx; 3) parapodium from middle of body; 4) seta (Yellow Sea).
Phyllodoce (Anaitides) papillosa Uschakov and Wu: 5) cephalic end, dorsal, with everted pharynx; 6) parapodium from middle of body (Yellow Sea).
Phyllodoce (Anaitides) madeirensis Langerhans: 7) parapodium of 10th segment; 8) parapodium from middle of body (Hainan).

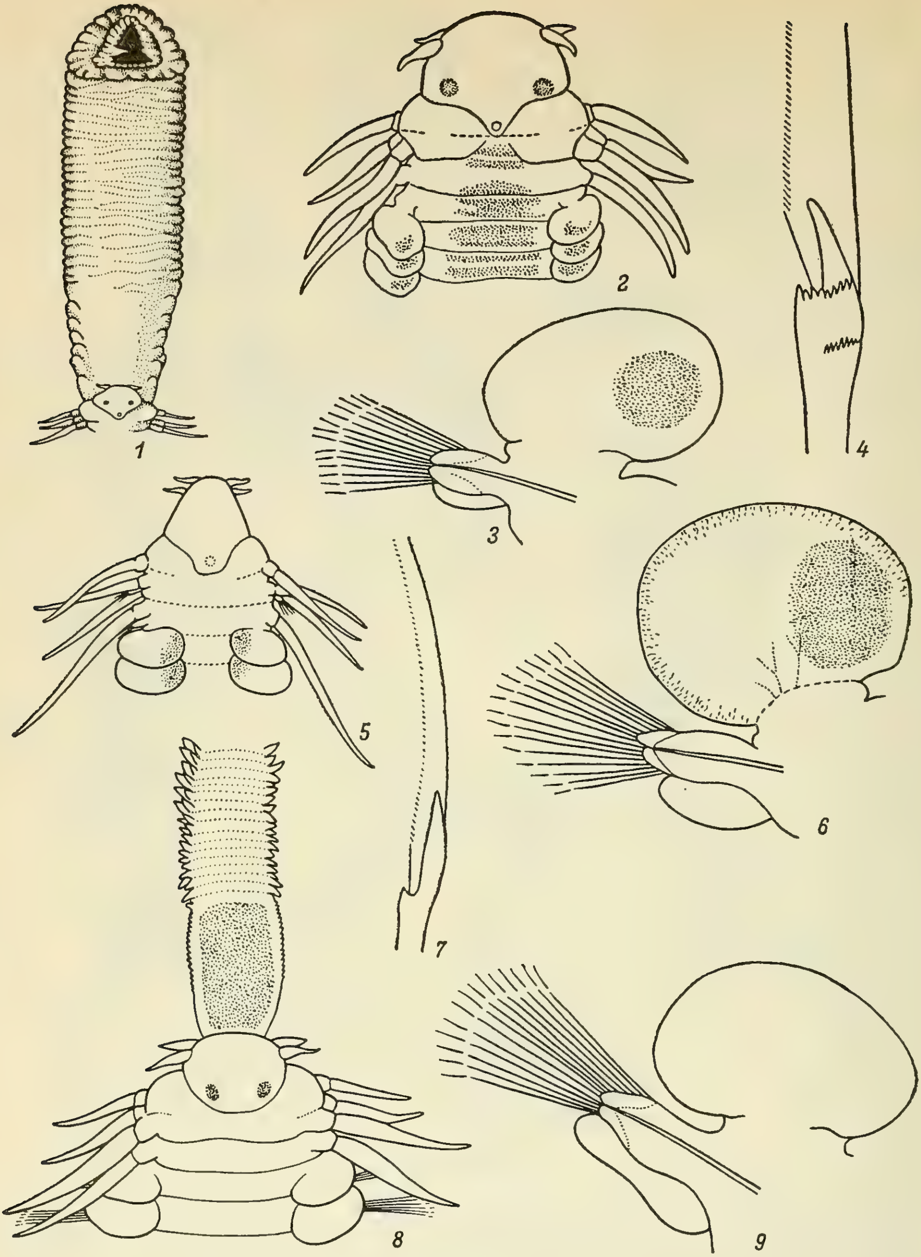

PLATE VII

Paranaitis polynoides (Moore): 1) everted pharynx; 2) cephalic end; 3) parapodium from middle of body; 4) articulation of seta (Southern Sakhalin).
Paranaitis caecum Uschakov: 5) cephalic end; 6) parapodium from middle of body; 7) seta (east of Honshu).
Paranaitis wahlbergi (Malmgren): 8) cephalic end, dorsal, with everted pharynx (only 1/10 of proboscis shown); 9) parapodium from middle of body (Novaya Zemlya).

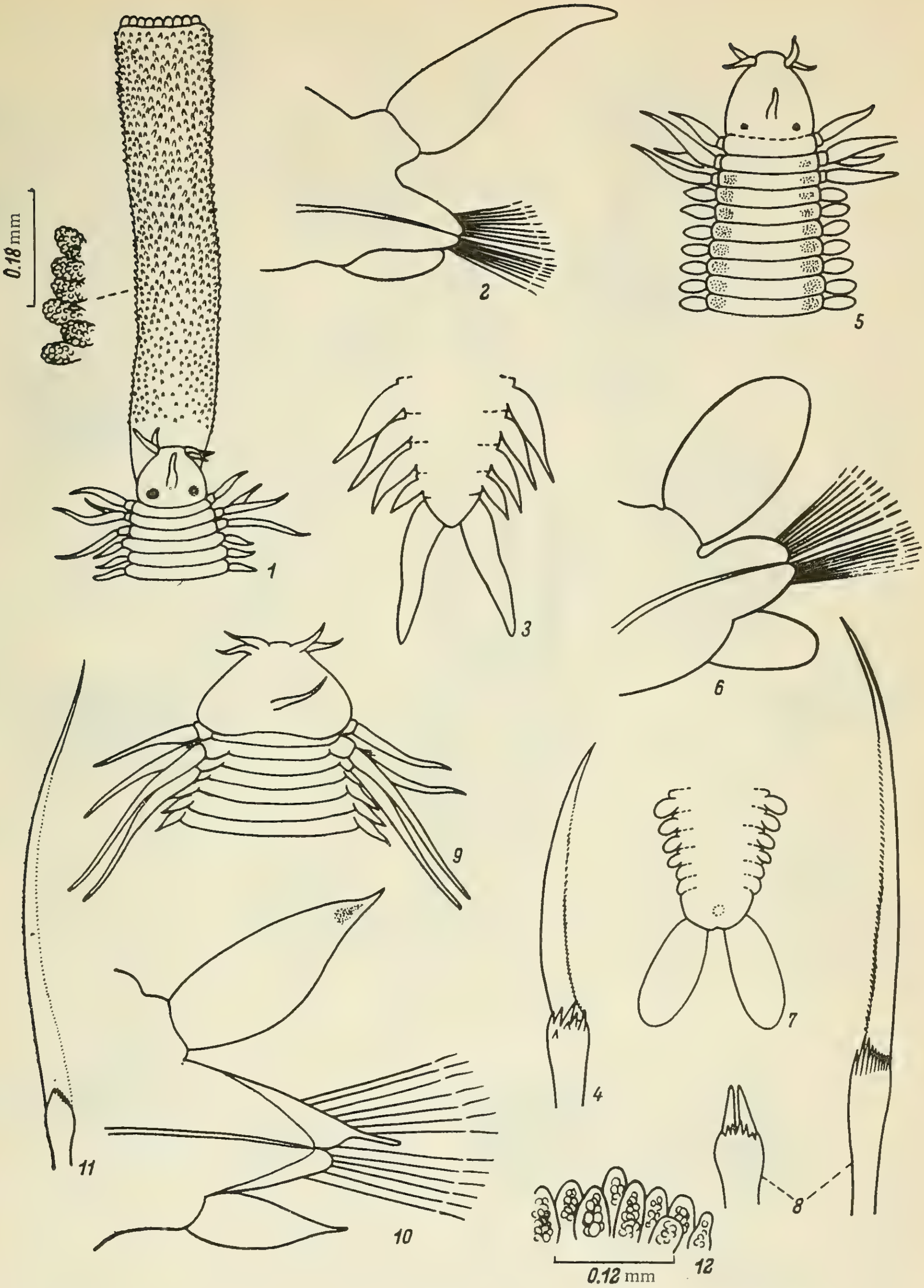

PLATE VIII

Eulalia viridis (L.): 1) cephalic end with everted pharynx and details of papillae of proboscis; 2) parapodium of 25th segment; 3) posterior end; 4) seta (Sea of Okhotsk).

Eulalia bilineata Johnston: 5) cephalic end; 6) parapodium of 25th segment; 7) posterior end; 8) seta (Sea of Japan).

Eulalia sigeformis Annenkova: 9) cephalic end; 10) parapodium from middle of body; 11) seta; 12) papillae on proboscis (Aleutian Depression).

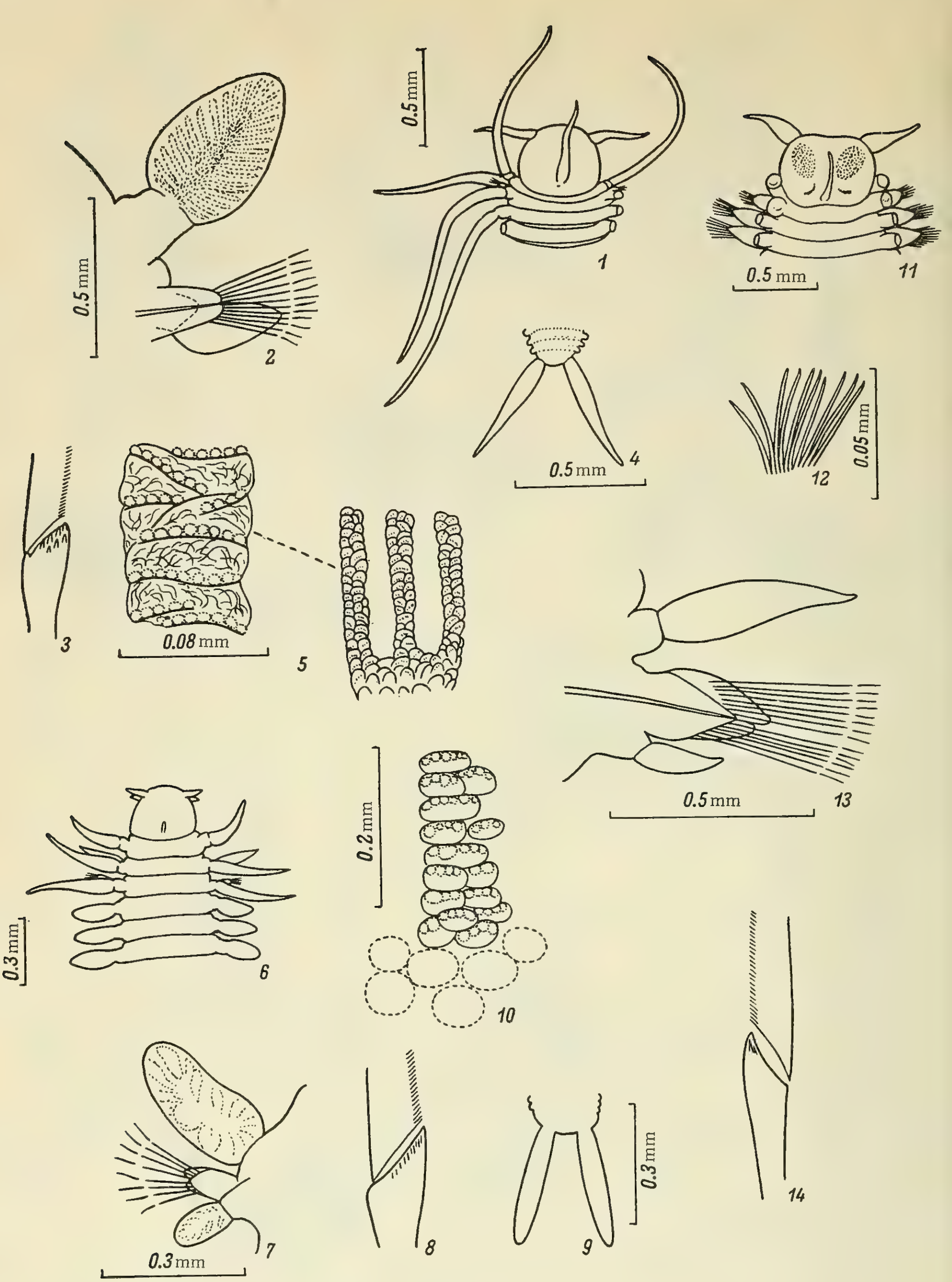

PLATE IX

Eulalia austrophylloformis Uschakov: 1) cephalic end; 2) parapodium of 38th segment; 3) seta; 4) pygidium with anal cirri; 5) longitudinal rows of papillae on distal part of proboscis (east of Honshu, type).
Eulalia gravieri Uschakov: 6) cephalic end; 7) parapodium of 25th segment; 8) seta; 9) pygidium with anal cirri; 10) papillae of longitudinal row on distal part of proboscis (east of Honshu, type).
Pterocirrus imajimai Uschakov: 11) cephalic end; 12) papillae on proboscis; 13) parapodium of 15th segment; 14) seta (California, type).

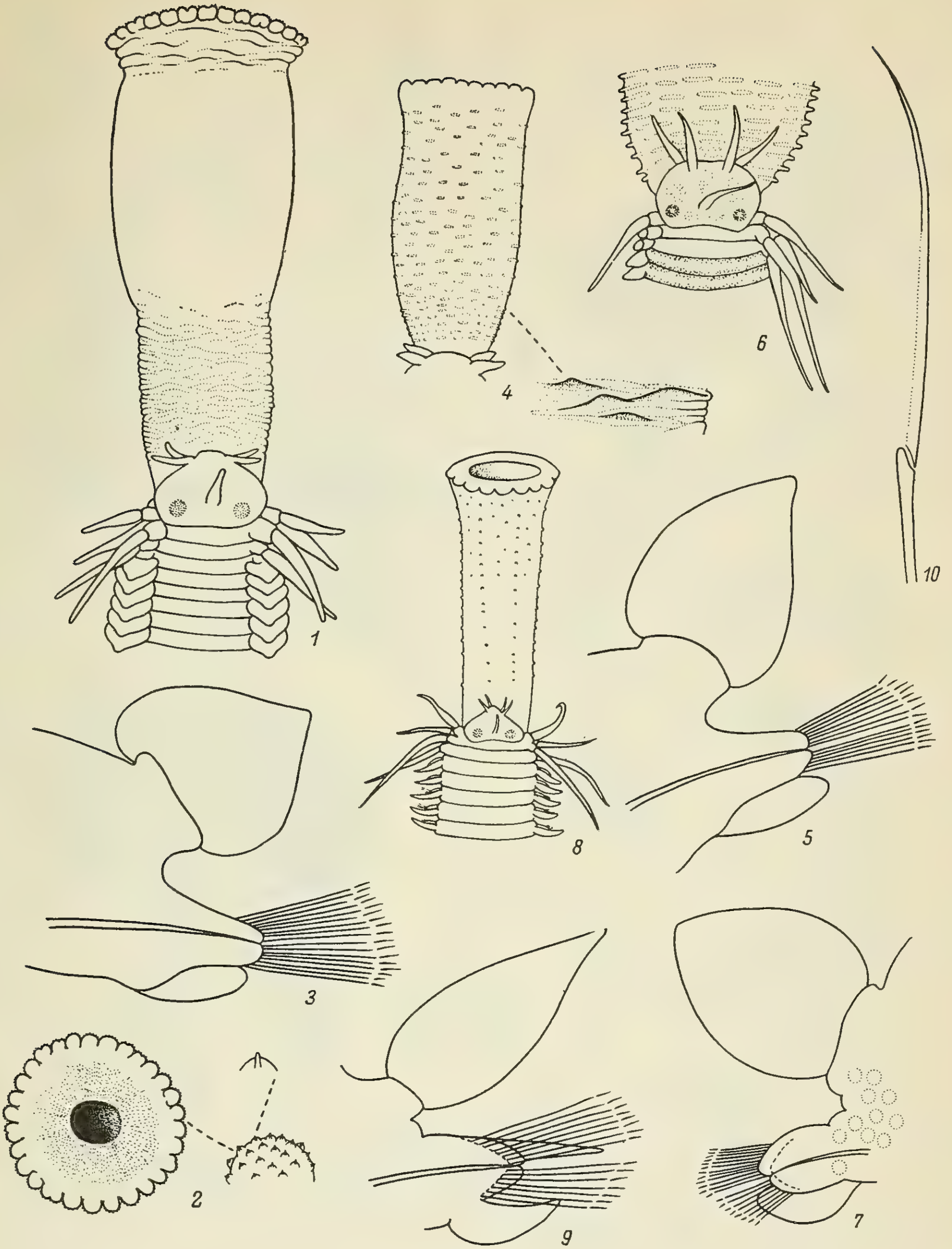

PLATE X

Eumida tubiformis Moore: 1) cephalic end, dorsal, with everted pharynx (proximal part of proboscis partly compressed); 2) distal end of proboscis, apical view, and details of marginal papillae; 3) parapodium from middle of body (Sea of Japan).

Eumida sanguinea (Oersted): 4) proboscis and detail of folds; 5) parapodium from middle of body (Sea of Japan).

Eumida albopicta (Marenzeller): 6) cephalic end and proximal part of proboscis; 7) parapodium from middle of body (Yellow Sea).

Eumida fusigera (Malmgren): 8) cephalic end with everted pharynx; 9) parapodium from middle of body; 10) seta (Oresund).

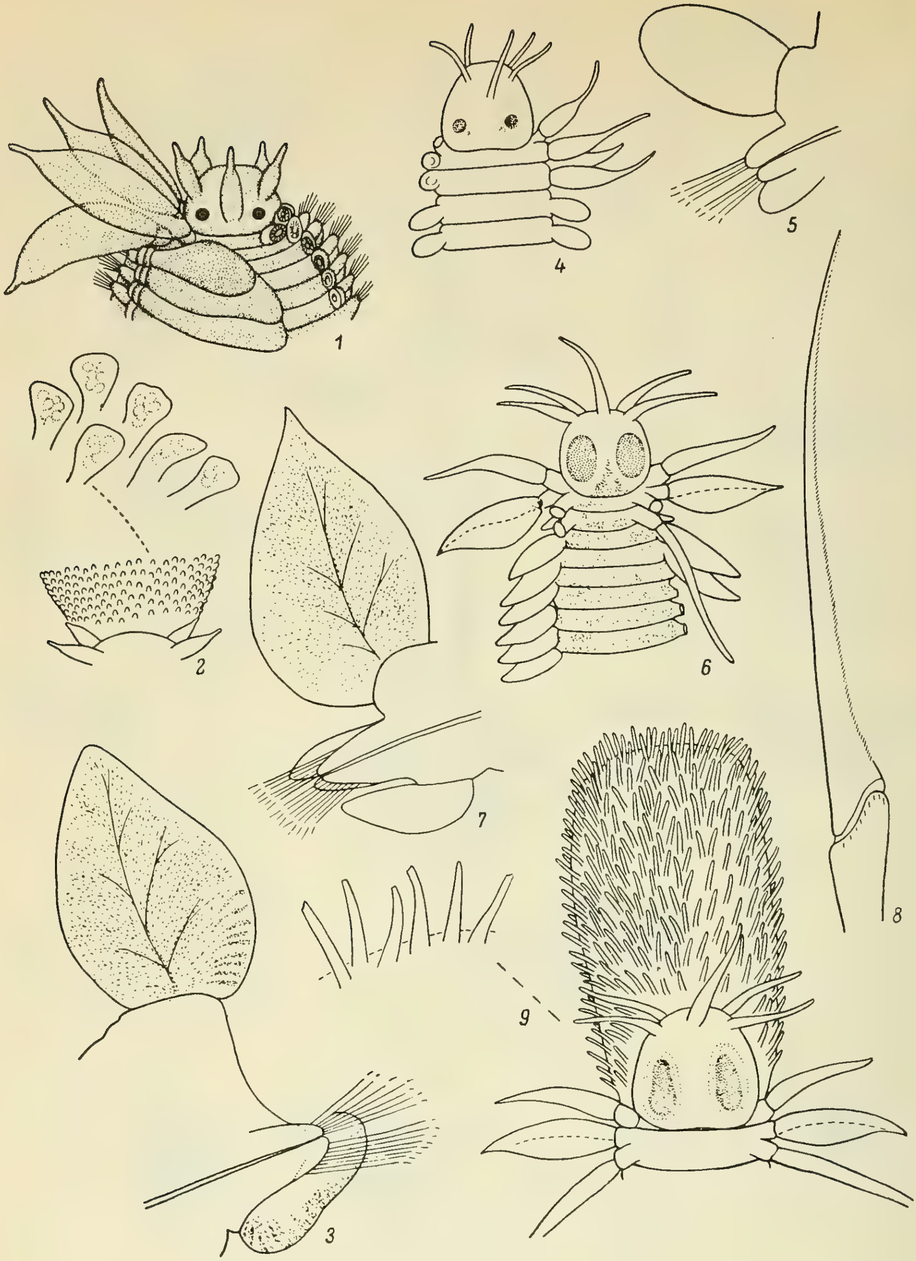

PLATE XI

Eumida nigrimaculata (Moore): 1) cephalic end, dorsal; 2) part of proboscis and papillae on proboscis; 3) parapodium from middle of body (Sea of Okhotsk).

Eumida minuta (Ditlevsen): 4) cephalic end, dorsal; 5) parapodium from middle of body (north of Novosibirskie Islands).

Pterocirrus macroceros (Grube): 6) cephalic end, dorsal; 7) parapodium from middle of body; 8) seta (Yellow Sea); 9) incompletely everted pharynx and papillae (Black Sea).

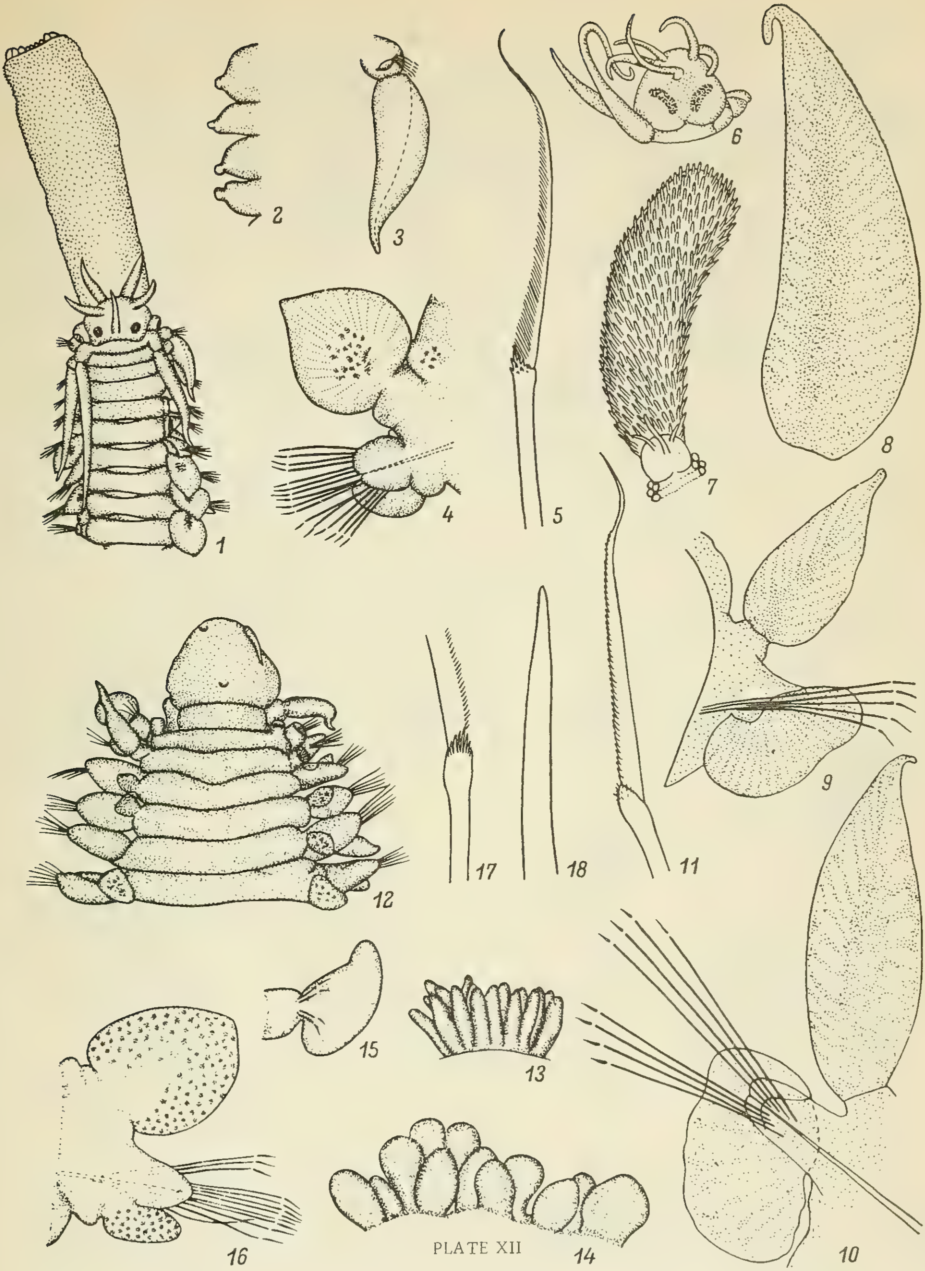

PLATE XII

Pterocirrus notoensis (Imajima): 1) cephalic end, dorsal, with everted pharynx; 2) papillae on proboscis; 3) ventral tentacular cirrus of 2nd segment; 4) parapodium of 25th segment; 5) seta (after Imajima, 1967).
Pterocirrus slastnikovi Annenkova: 6) cephalic end, dorsal; 7) proboscis; 8) ventral tentacular cirrus of 2nd segment; 9) parapodium of anterior segments; 10) parapodium of middle segments; 11) seta (after Annenkova, 1946).
Steggoa pacifica Imajima: 12) cephalic end, dorsal; 13) papillae on proximal part of proboscis; 14) papillae on distal part of proboscis; 15) ventral cirrus of 2nd segment; 16) parapodium of 20th segment; 17) segmented seta; 18) aciculum (after Imajima, 1964).

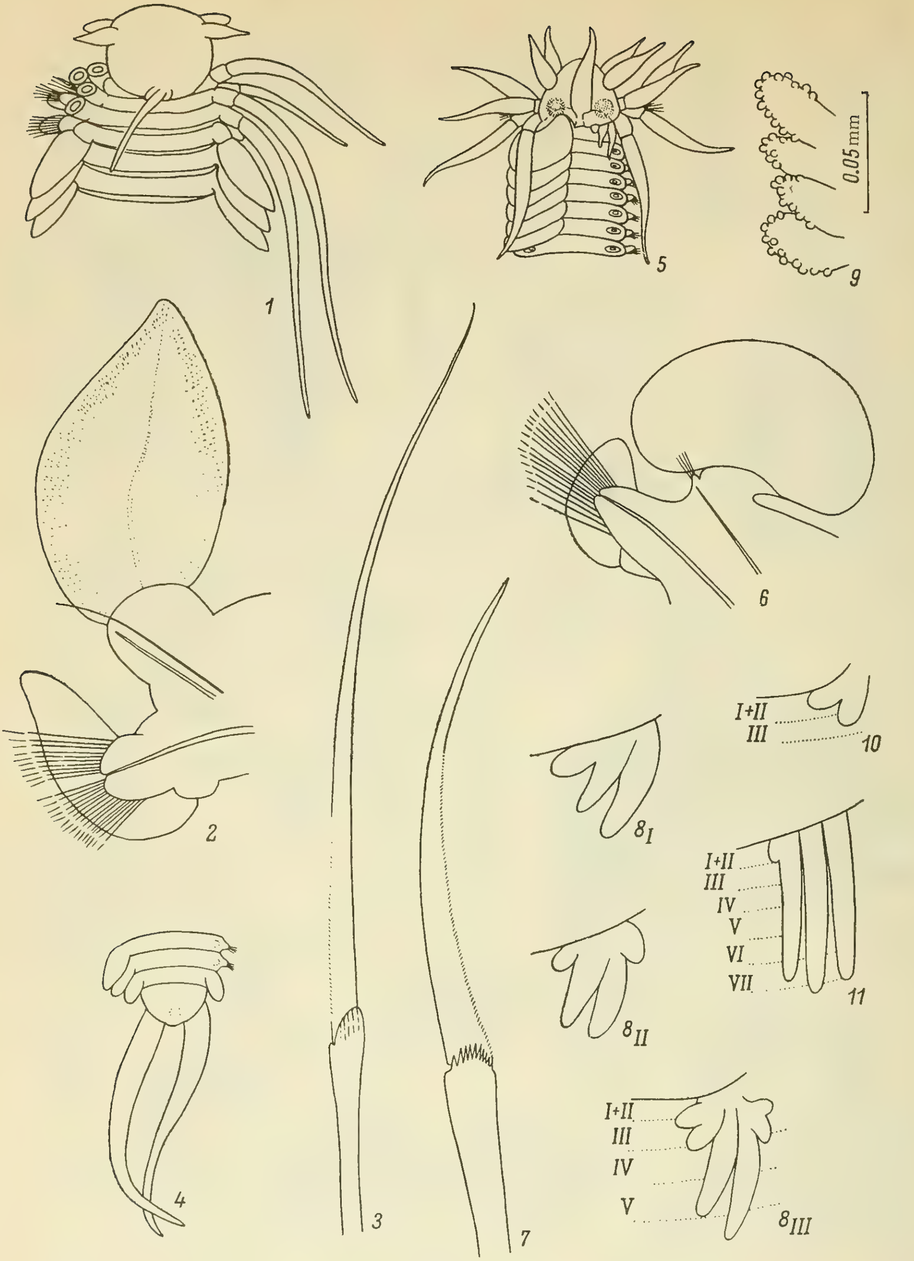

PLATE XIII

Austrophyllum sphaerocephala (Levenstein): 1) cephalic end, dorsal; 2) parapodium from middle of body; 3) seta; 4) posterior end (Kuril - Kamchatka Trench).
Notophyllum imbricatum Moore: 5) cephalic end, dorsal; 6) parapodium from middle of body; 7) seta; 8) nuchal organ; 9) lateral papillae on proboscis, from the side (Sea of Japan).
Notophyllum foliosum (Sars): 10) nuchal organ (Bering Island).
Notophyllum splendens (Schmarda): 11) nuchal organ (Yellow Sea).

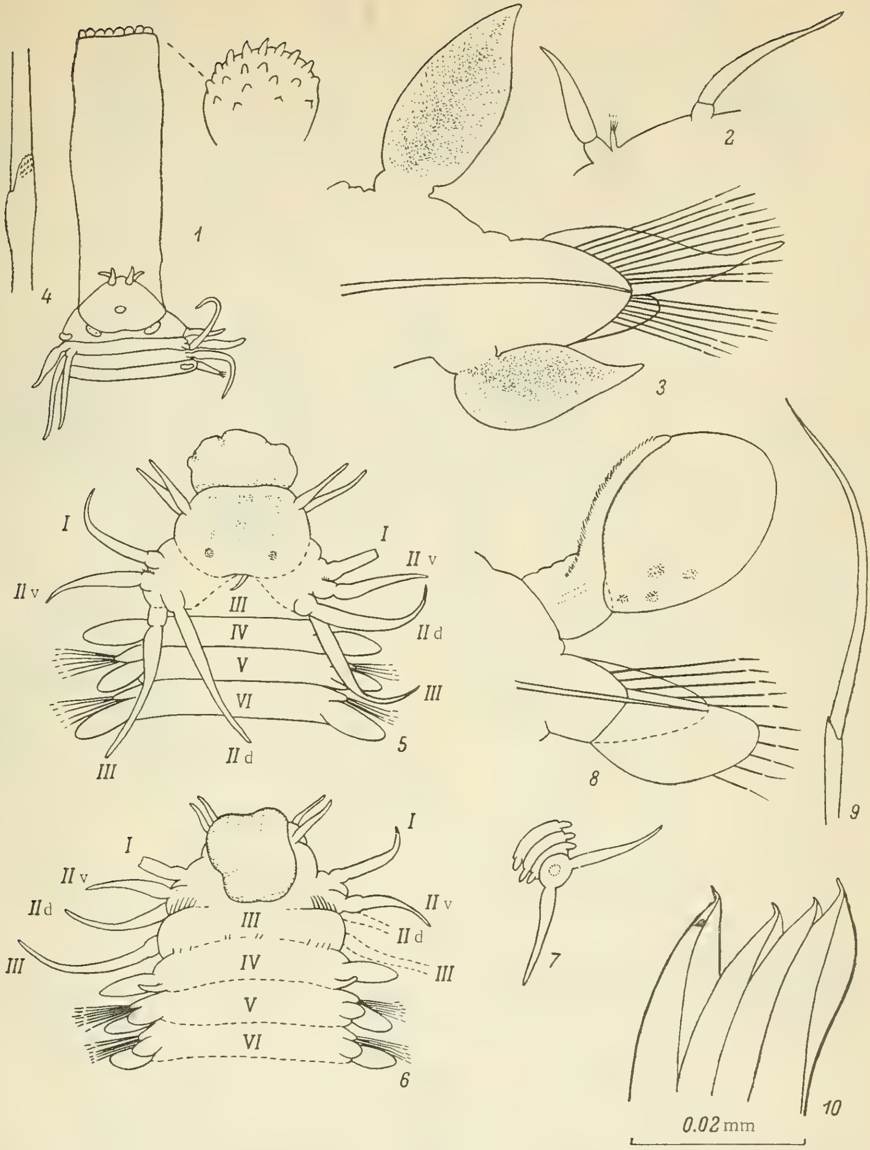

PLATE XIV

Vitiazia dogieli Uschakov: 1) cephalic end with everted pharynx; 2) tentacular cirri of 2nd segment; 3) parapodium from middle of body; 4) seta (Kuril - Kamchatka Trench).
Chaetoparia nilssoni Malmgren: 5) cephalic end, dorsal, with partly everted pharynx; 6) cephalic end, ventral; 7) pygidium; 8) parapodium from middle of body; 9) segmented seta of normal parapodia; 10) simple seta of 3rd segment (west coast of Sweden).

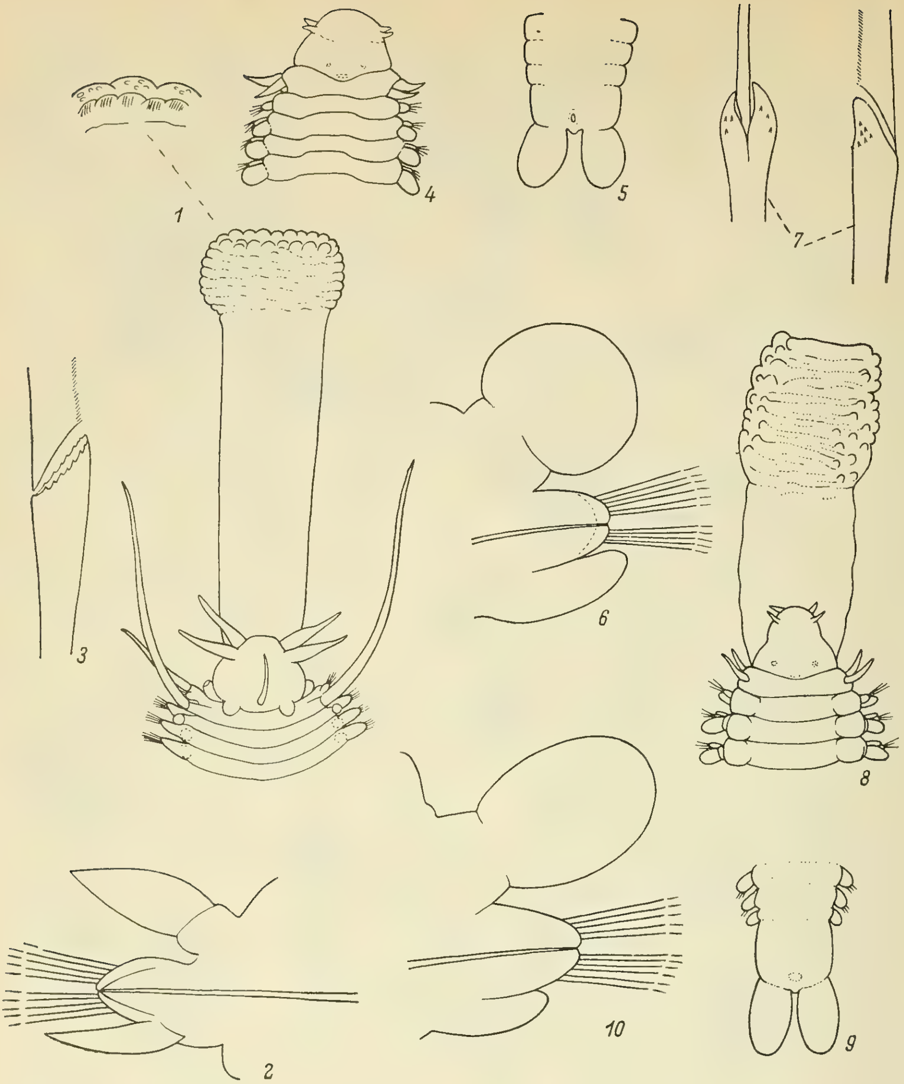

PLATE XV

Vitiaziphyllum nuchalum Uschakov: 1) cephalic end with everted proboscis and detail of papillae; 2) parapodium from middle of body; 3) articulation of seta (east of Honshu, type).

Eteone flava (Fabricius): 4) cephalic end; 5) posterior end; 6) 20th parapodium; 7) seta, frontal and lateral (Barents Sea).

Eteone longa (Fabricius): 8) cephalic end with everted pharynx; 9) posterior end; 10) 20th parapodium (White Sea).

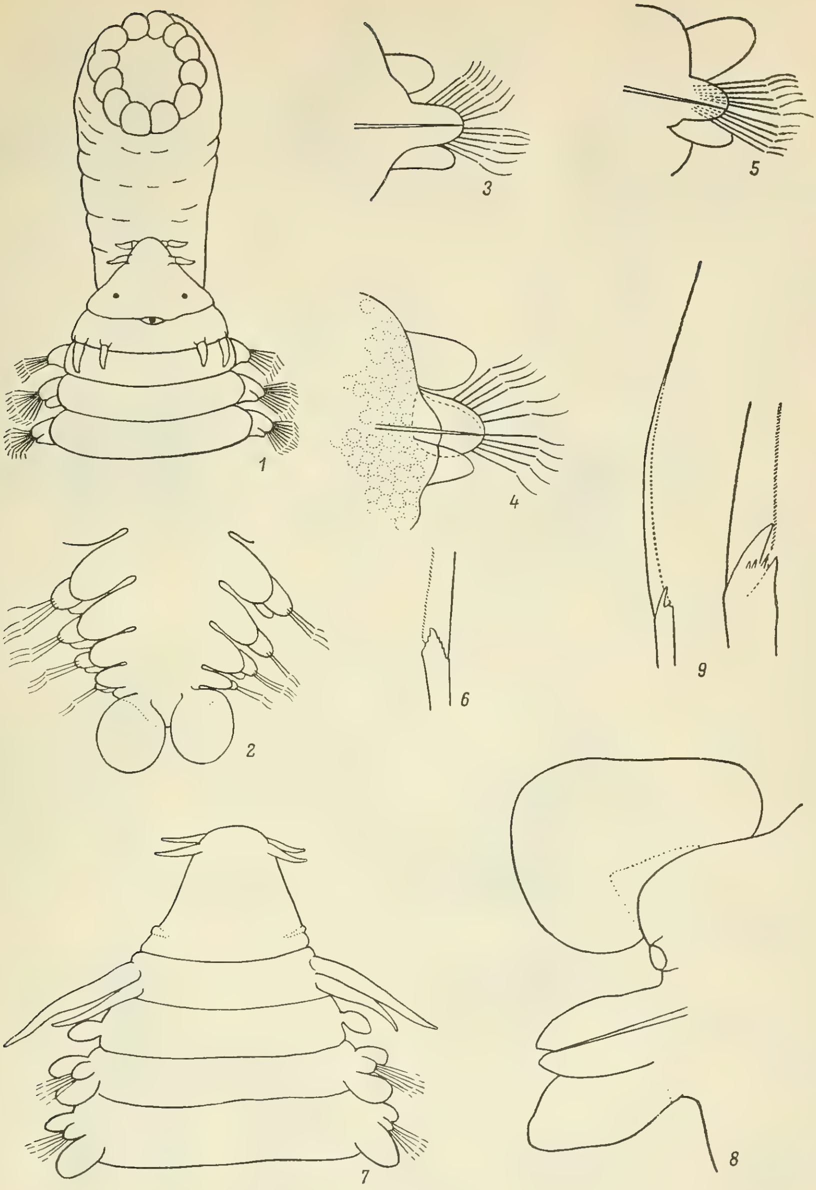

PLATE XVI

Eteone delta Wu and Chen: 1) cephalic end with everted pharynx; 2) posterior end; 3) 6th parapodium; 4) 40th parapodium; 5) 100th parapodium; 6) seta (delta of Yangtse River, after Wu Pao-ling and Chen, 1963).

Eteone lactea Claparède: 7) cephalic end; 8) parapodium from middle of body; 9) seta (Oresund).

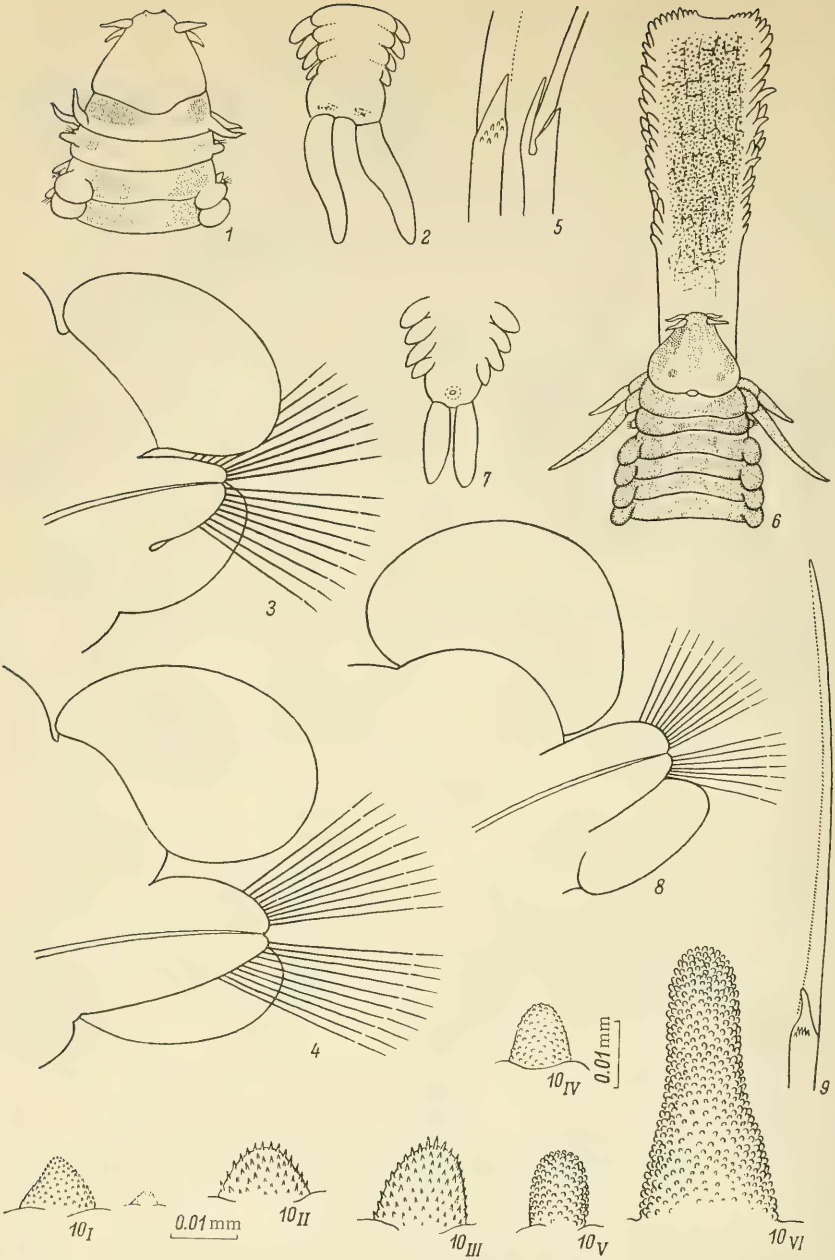

PLATE XVII

Eteone spetsbergensis bistriata Uschakov: 1) cephalic end; 2) posterior end; 3) 40th parapodium; 4) 90th parapodium; 5) seta (Sea of Japan).

Eteone (Mysta) barbata (Malmgren): 6) cephalic end with everted pharynx; 7) posterior end; 8) 40th parapodium; 9) seta; 10) small papillae on proboscis (Oresund – 10_{I}, White Sea – 10_{II}, Sea of Okhotsk – 10_{III}, Bering Strait – 10_{IV}, Aniva Bay – 10_{V}, northern Kuril Islands – 10_{VI}).

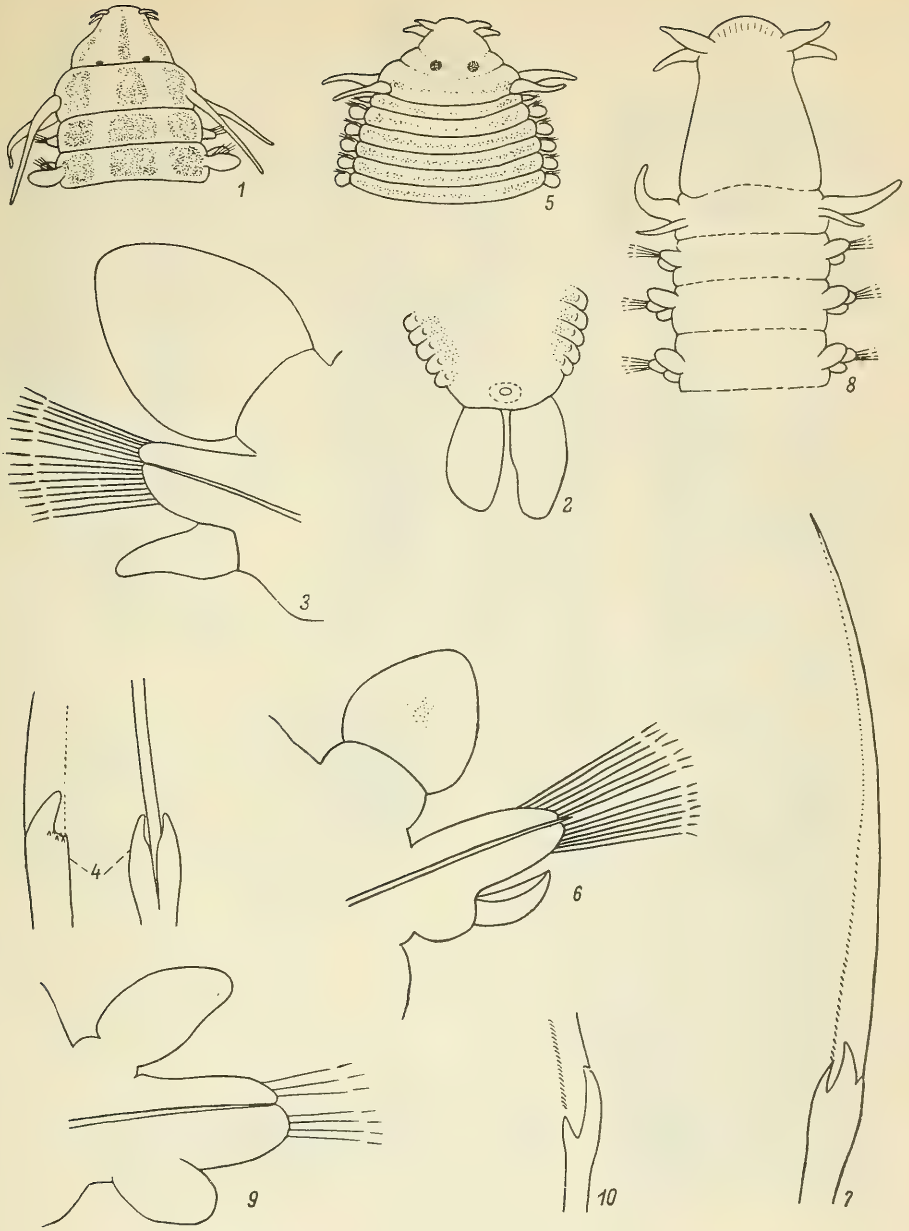

PLATE XVIII

Eteone (Mysta) ornata Grube: 1) cephalic end; 2) posterior end; 3) parapodium from middle of body; 4) seta (Sea of Japan).
Eteone (Mysta) maculata (Treadwell): 5) cephalic end; 6) parapodium from middle of body (25th segment); 7) seta (Gulf of Tonkin).
Eteone vitiazi Uschakov: 8) cephalic end; 9) parapodium, 33rd segment; 10) seta (east of Honshu, type).

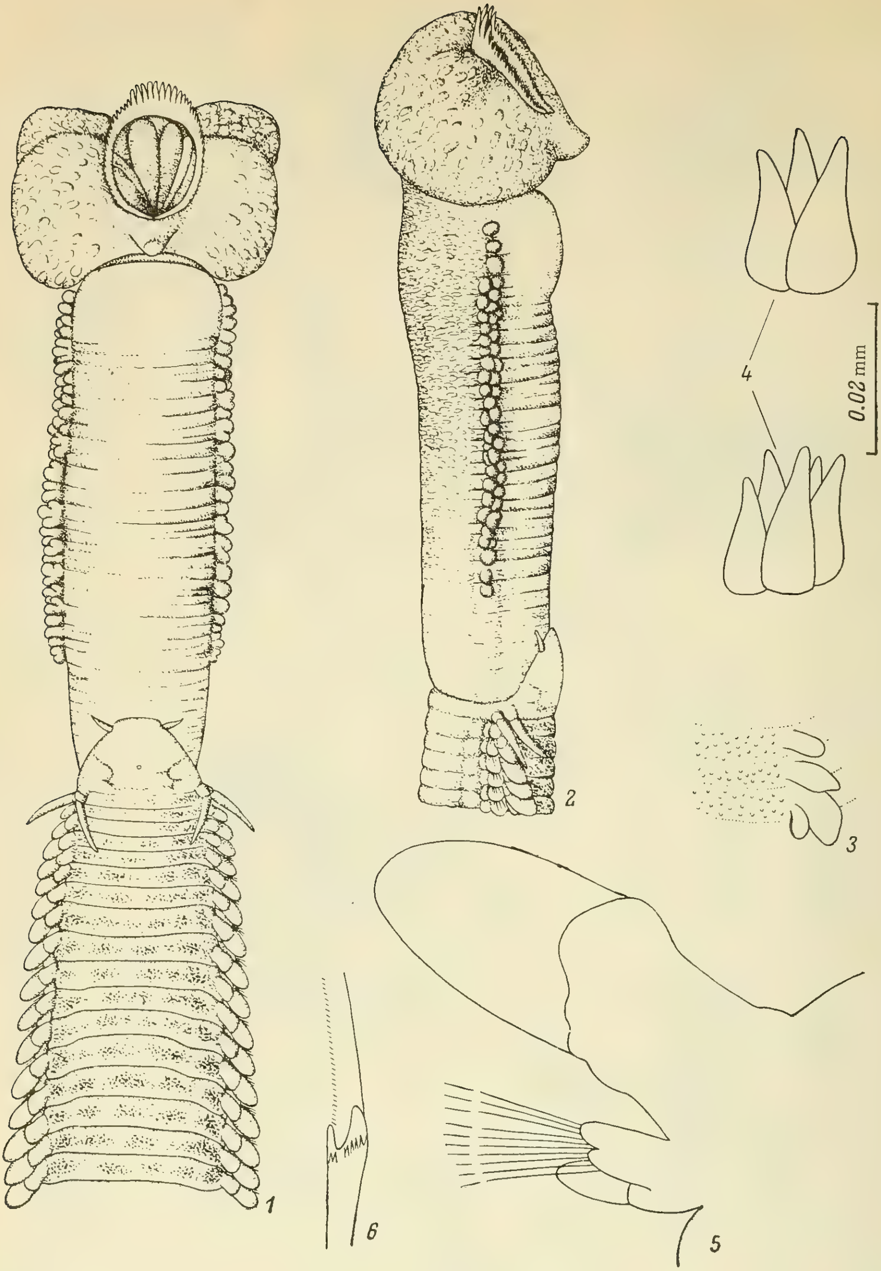

PLATE XIX

Eteone (Mysta) tchangsii Uschakov and Wu: 1) cephalic end with everted pharynx, dorsal; 2) same, lateral; 3) part of proboscis; 4) spines on dorsal side of proboscis; 5) parapodium from middle of body; 6) seta (Yellow Sea).

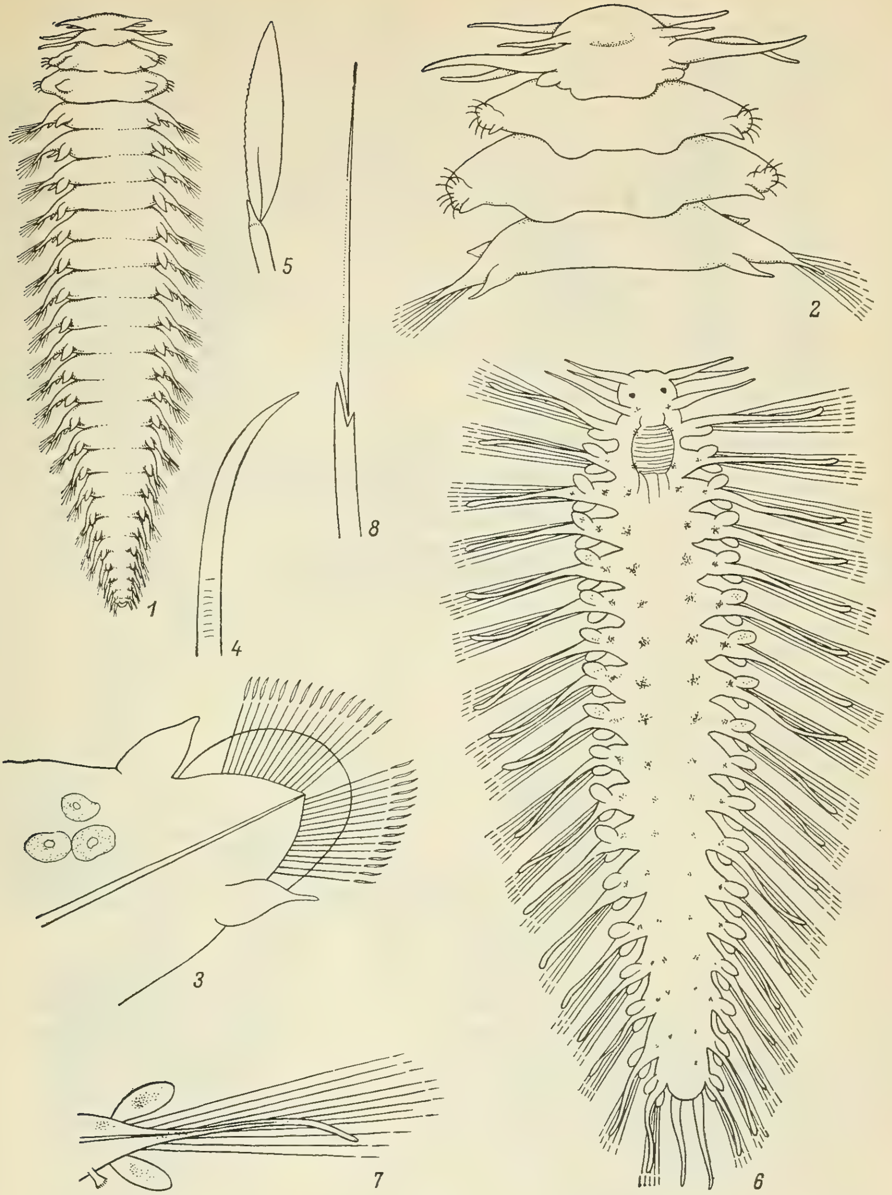

PLATE XX

Lopadorhynchus appendiculatus Southern: 1) general view, dorsal; 2) cephalic end, ventral; 3) parapodium, 10th segment; 4) hook-shaped seta of parapodia of 1st—2nd setose segments; 5) segmented seta (southeast of the Kuril Islands).

Pontodora pelagica Greeff; 6) general view, dorsal; 7) parapodium; 8) seta (southeast of the Kuril Islands).

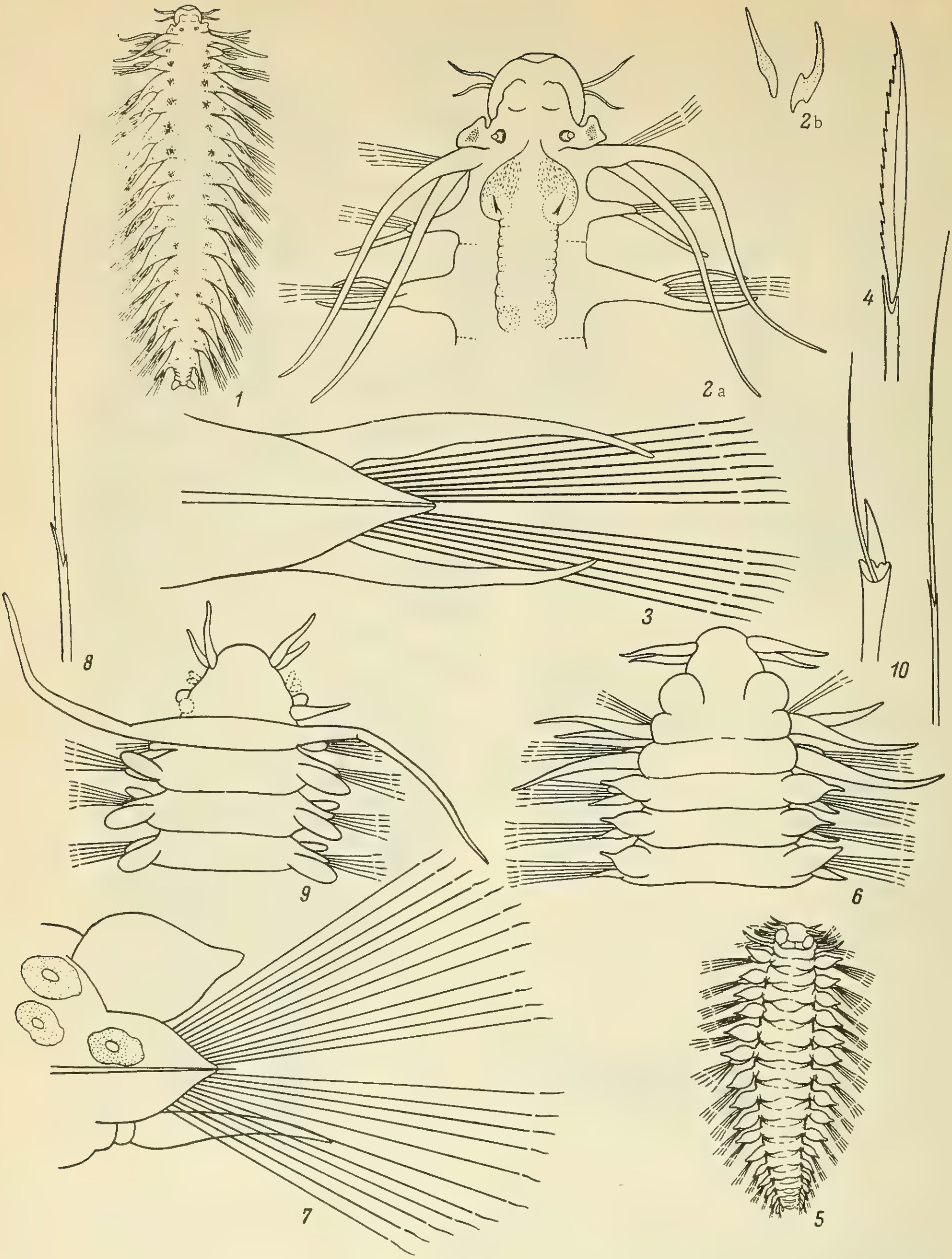

PLATE XXI

Pelagobia longicirrata Greeff: 1) general view, dorsal; 2a) cephalic end, dorsal; 2b) jaws; 3) parapodium; 4) seta (Northwest Pacific).

Maupasia caeca Viguier: 5) general view, dorsal (after Tebble, 1962); 6) cephalic end, dorsal; 7) parapodium from middle of body; 8) seta (Northwest Pacific).

Maupasia brodskyi Uschakov: 9) cephalic end, dorsal; 10) thick and thin segmented setae (Northwest Pacific).

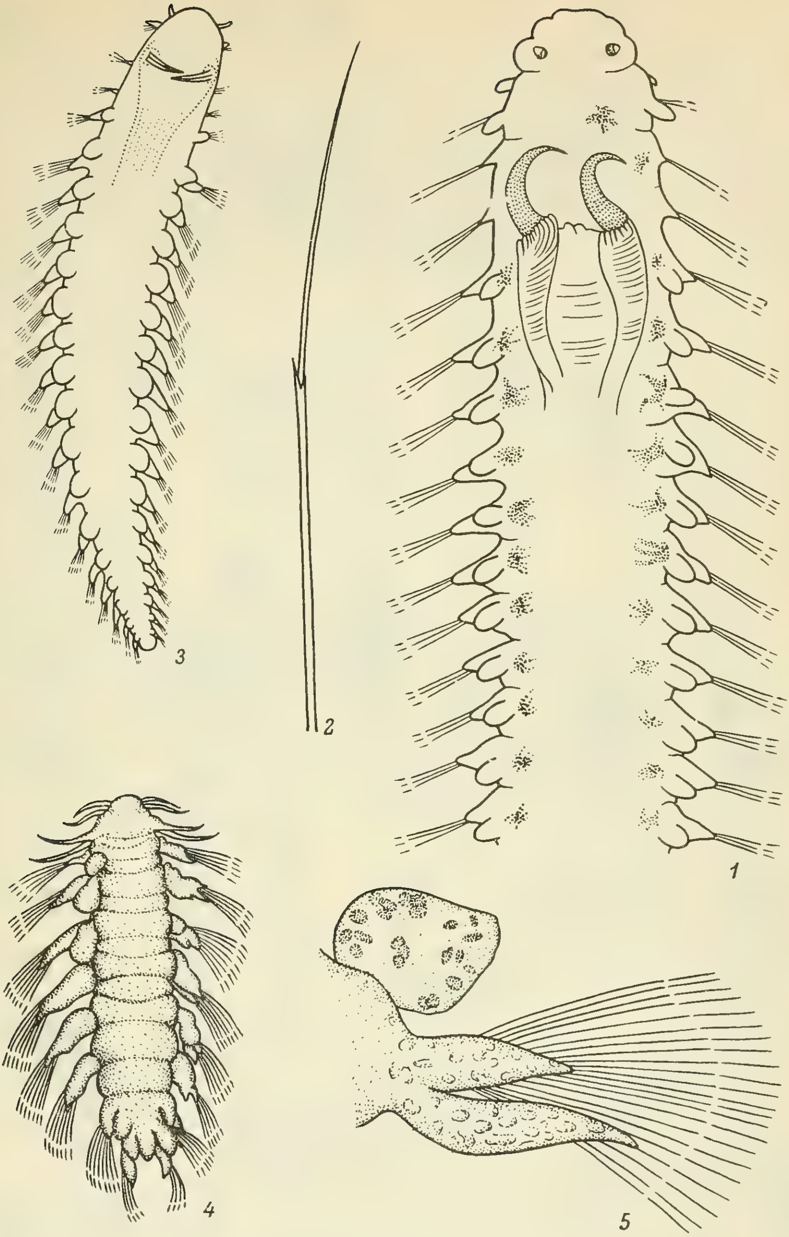

PLATE XXII

Phalacrophorus pictus pictus Greeff: 1) cephalic end, dorsal; 2) seta (Polar Basin).
Phalacrophorus pictus borealis Reibisch: 3) general view, dorsal (Polar Basin).
Pedinosoma curtum Reibisch: 4) general view, dorsal; 5) parapodium (after Tebble, 1962).

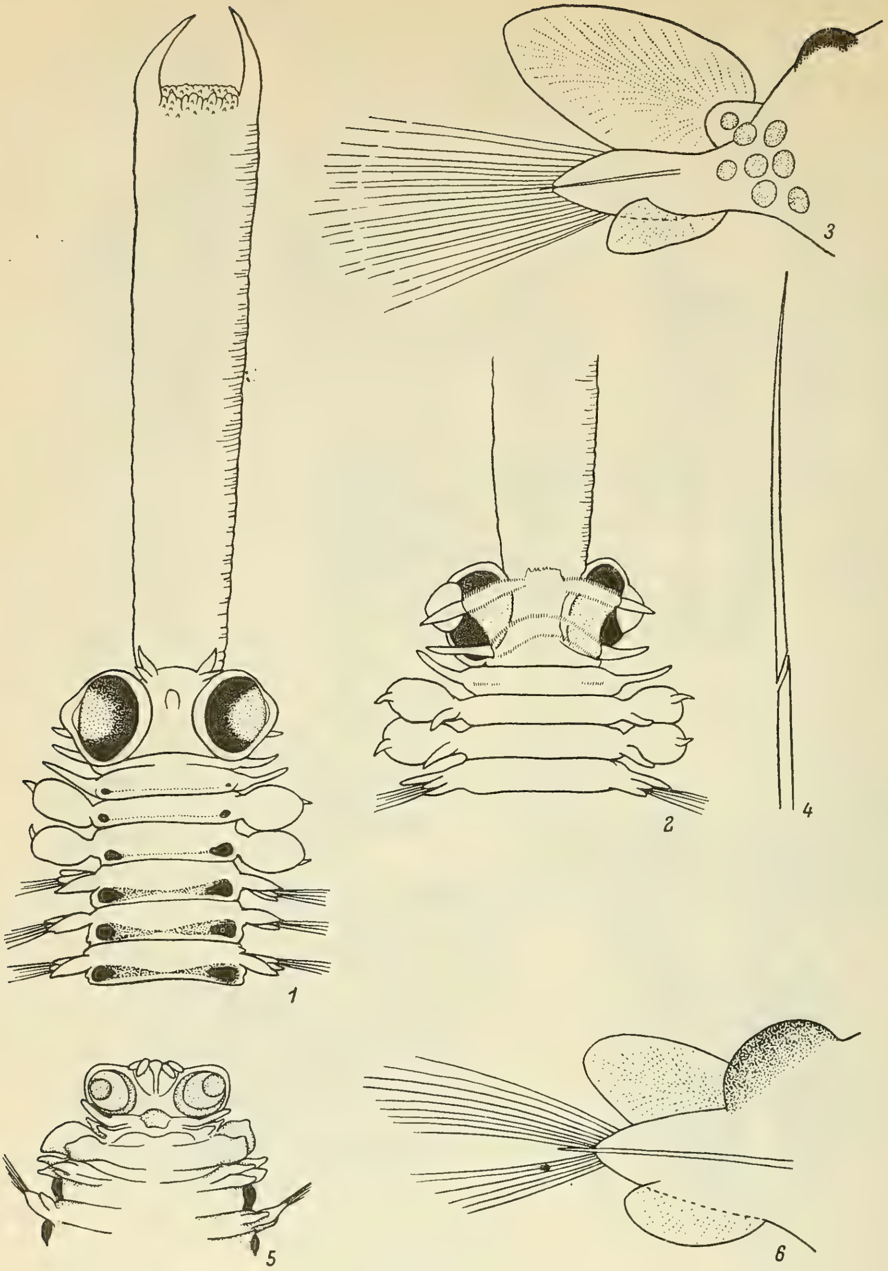

PLATE XXIII

Torrea candida (Delle-Chiaje): 1) cephalic end of female with everted pharynx, dorsal; 2) same, ventral; 3) parapodium from middle of body; 4) seta (Mediterranean).
Naiades cantrainii Delle-Chiaje: 5) cephalic end (after Dales, 1957); 6) parapodium (Bay of Bengal).

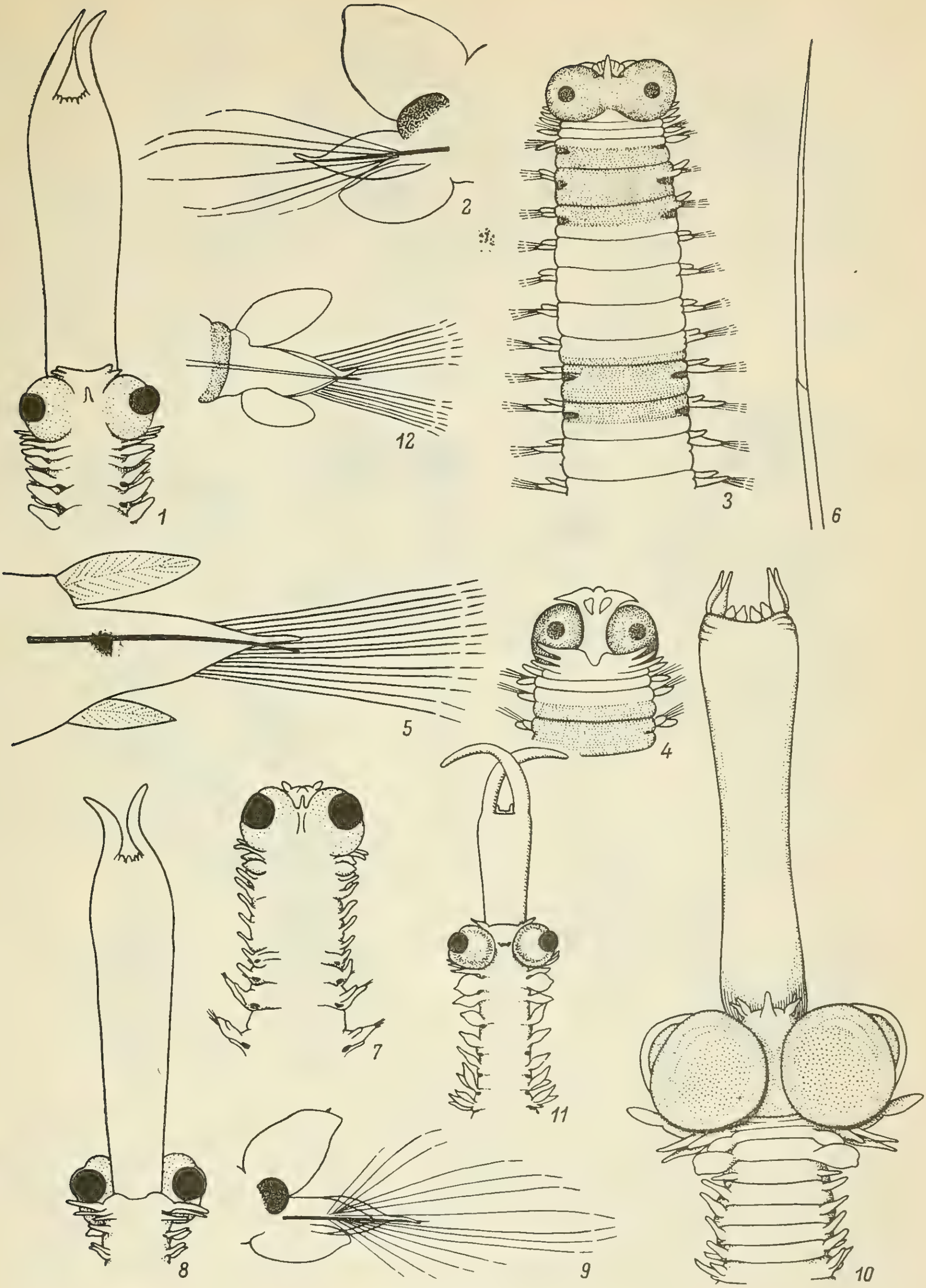

PLATE XXIV

Vanadis formosa Claparède: 1) cephalic end, dorsal; 2) parapodium (after Dales, 1957).
Vanadis longissima (Levinsen): 3) cephalic end, dorsal; 4) same, ventral; 5) parapodium; 6) seta (Northwest Pacific).
Vanadis crystallina Greeff: 7) cephalic end, dorsal; 8) same, ventral; 9) parapodium (after Dales, 1957).
Vanadis tagensis Dales: 10) cephalic end, dorsal (after Dales, 1955).
Vanadis minuta Treadwell: 11) cephalic end, dorsal (after Dales, 1957); 12) parapodium (Bay of Bengal).

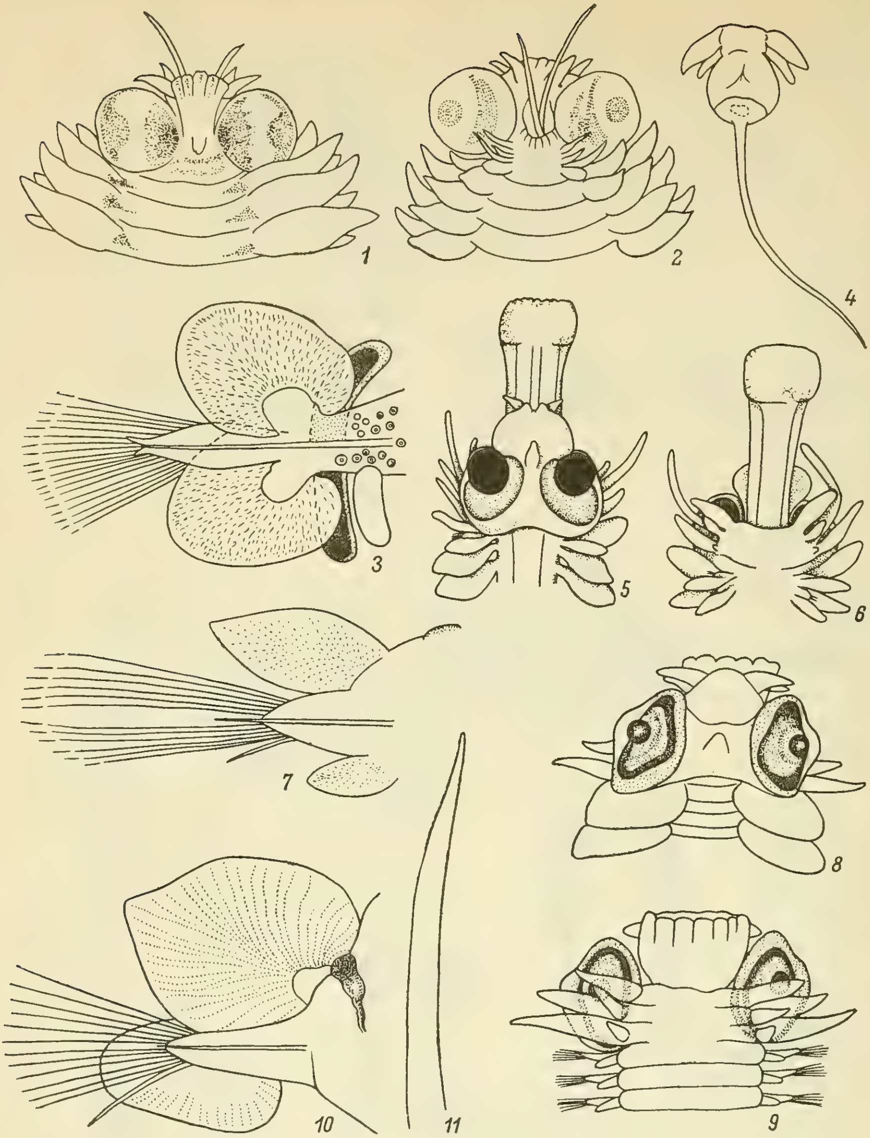

PLATE XXV

Alciopa reynaudii Aud. and M.-Edw.: 1) cephalic end, dorsal; 2) same, ventral; two cirriform processes of retracted pharynx projecting from mouth; 3) parapodium; 4) pygidium, with anal cirrus (Northwest Pacific).
Plotohelmis tenuis (Apstein): 5) cephalic end, dorsal; 6) same, ventral (after Dales, 1957); 7) parapodium (Hainan).
Alciopina parasitica Claparède and Panceri: 8) cephalic end, dorsal; 9) same, ventral; 10) parapodium; 11) acicular seta (Northwest Pacific).

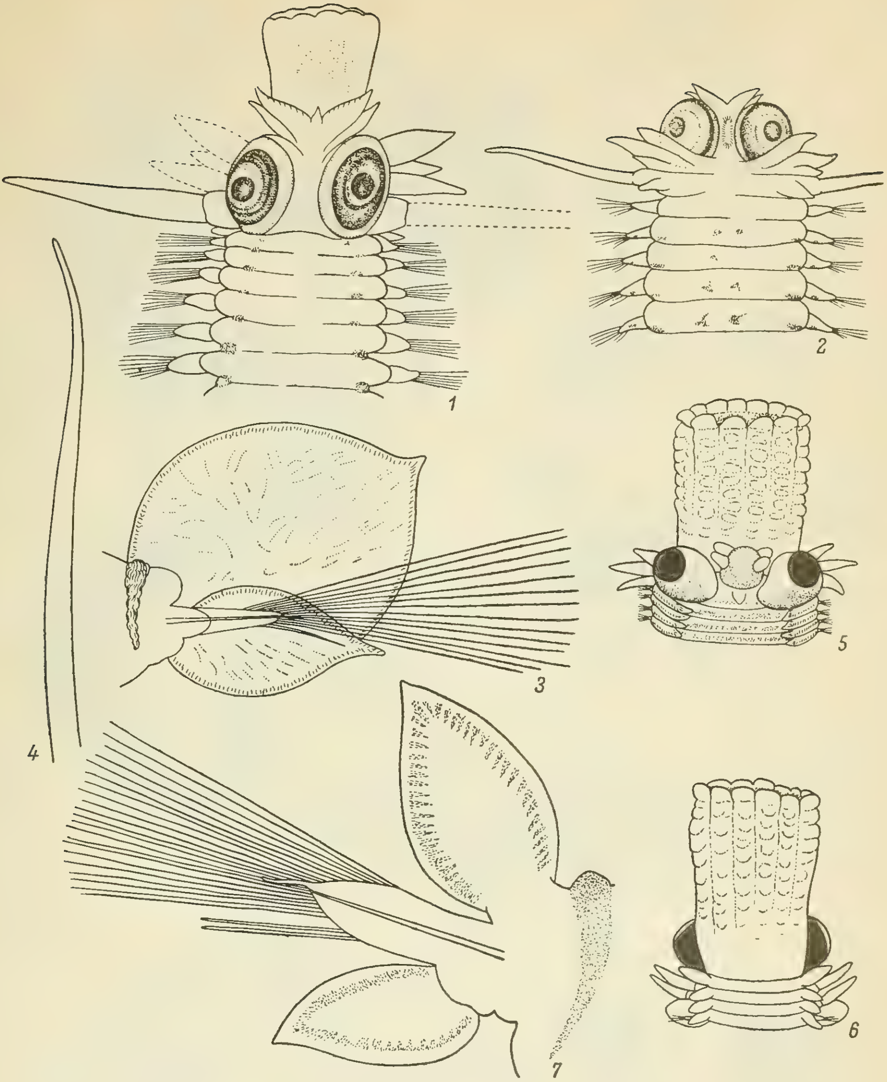

PLATE XXVI

Krohnia lepidota (Krohn): 1) cephalic end with everted pharynx, dorsal (dorsal cirri not shown); 2) same, ventral (pharynx retracted); 3) parapodium; 4) acicular seta (Northwest Pacific).
Krohnia excellata (Uschakov): 5) cephalic end with everted pharynx, dorsal; 6) same, ventral; 7) parapodium (Northwest Pacific).

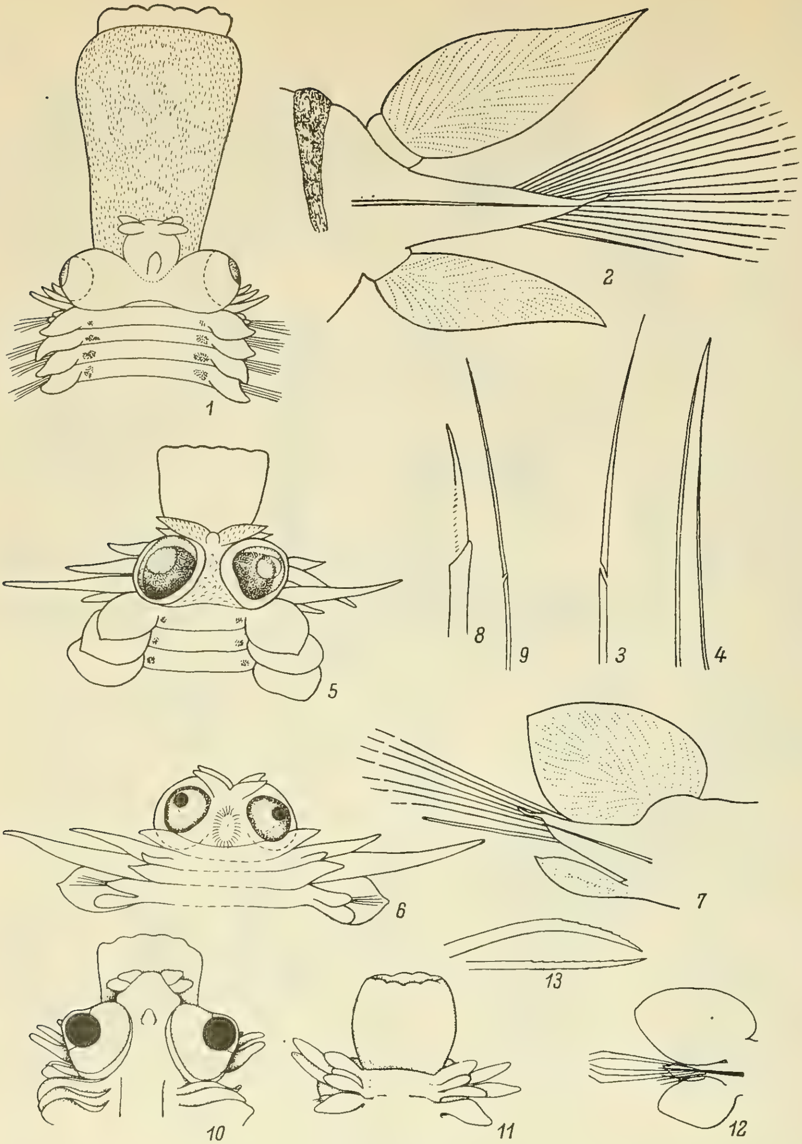

PLATE XXVII

Rhynchonerella gracilis Costa: 1) cephalic end with everted pharynx, dorsal; 2) parapodium; 3) segmented seta; 4) acicular seta (Northwest Pacific).

Rhynchonerella petersii (Langerhans): 5) cephalic end with everted pharynx, dorsal; 6) same, ventral (pharynx retracted); 7) parapodium; 8) ventral, short, segmented seta; 9) dorsal, thin, segmented seta (Northwest Pacific).

Rhynchonerella mobii (Apstein): 10) cephalic end with everted pharynx, dorsal; 11) same, ventral; 12) parapodium; 13) acicular setae (after Dales, 1957).

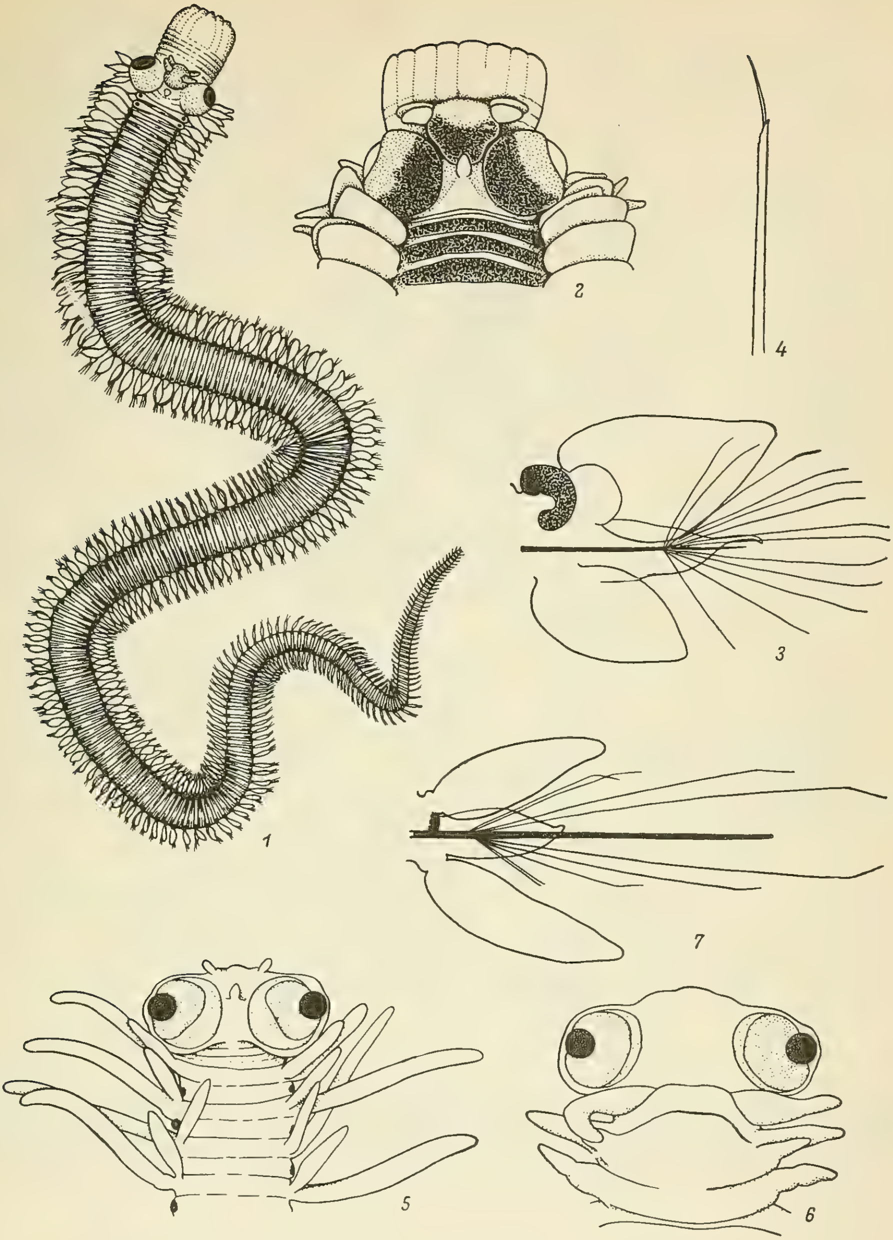

PLATE XXVIII

Rhynchonerella angelini (Kinberg): 1) general (after Tebble, 1962); 2) cephalic end, dorsal; 3) parapodium; 4) seta (after Dales, 1957).
Watelio gravieri (Benham): 5) cephalic end, adult, dorsal; 6) same, ventral, juvenile; 7) parapodium from anterior part of body (after Dales, 1957).

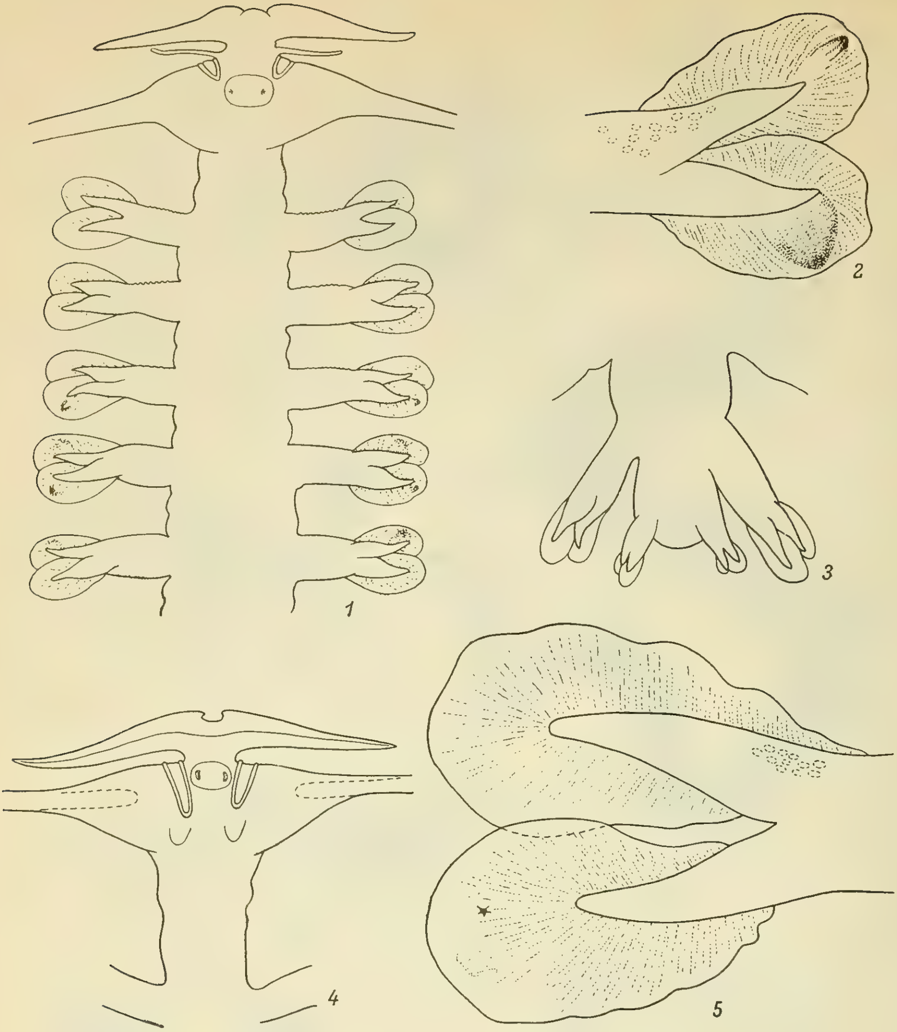

PLATE XXIX

Tomopteris elegans Chun: 1) cephalic end, dorsal; 2) 4th parapodium; 3) posterior end (Northwest Pacific).

Tomopteris septentrionalis Quatrefages: 4) cephalic end, dorsal; 5) 8th parapodium (Northwest Pacific).

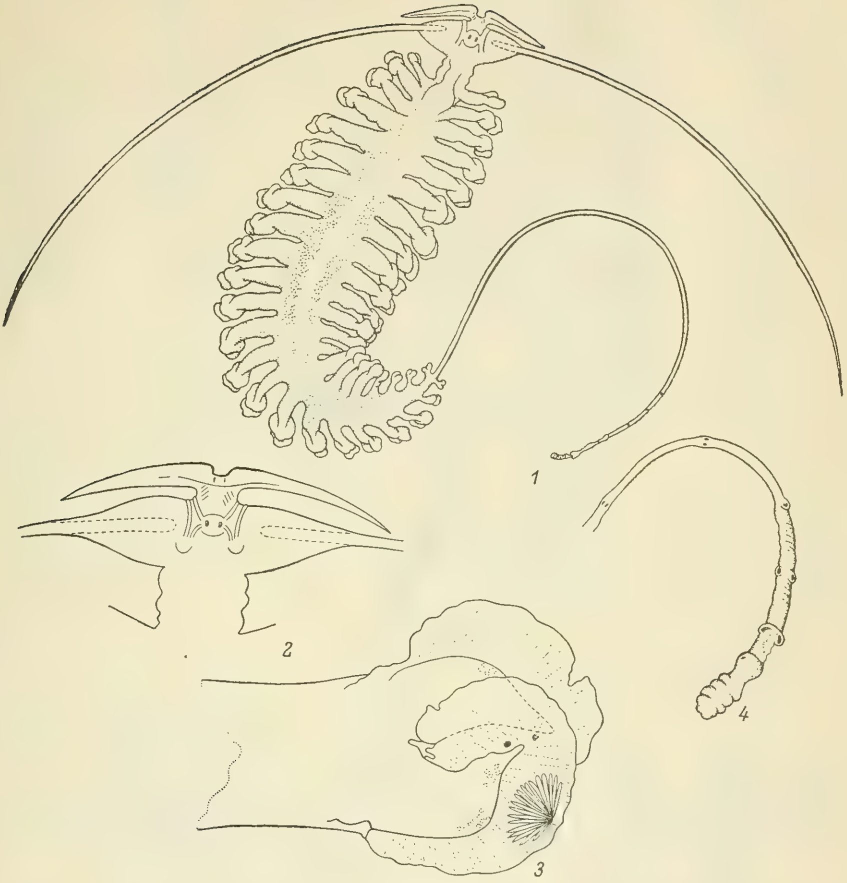

PLATE XXX

Tomopteris (Johnstonella) pacifica Izuka: 1) general view, dorsal (×2); 2) cephalic end, dorsal; 3) 8th parapodium; 4) terminal part of tail (Northwest Pacific).

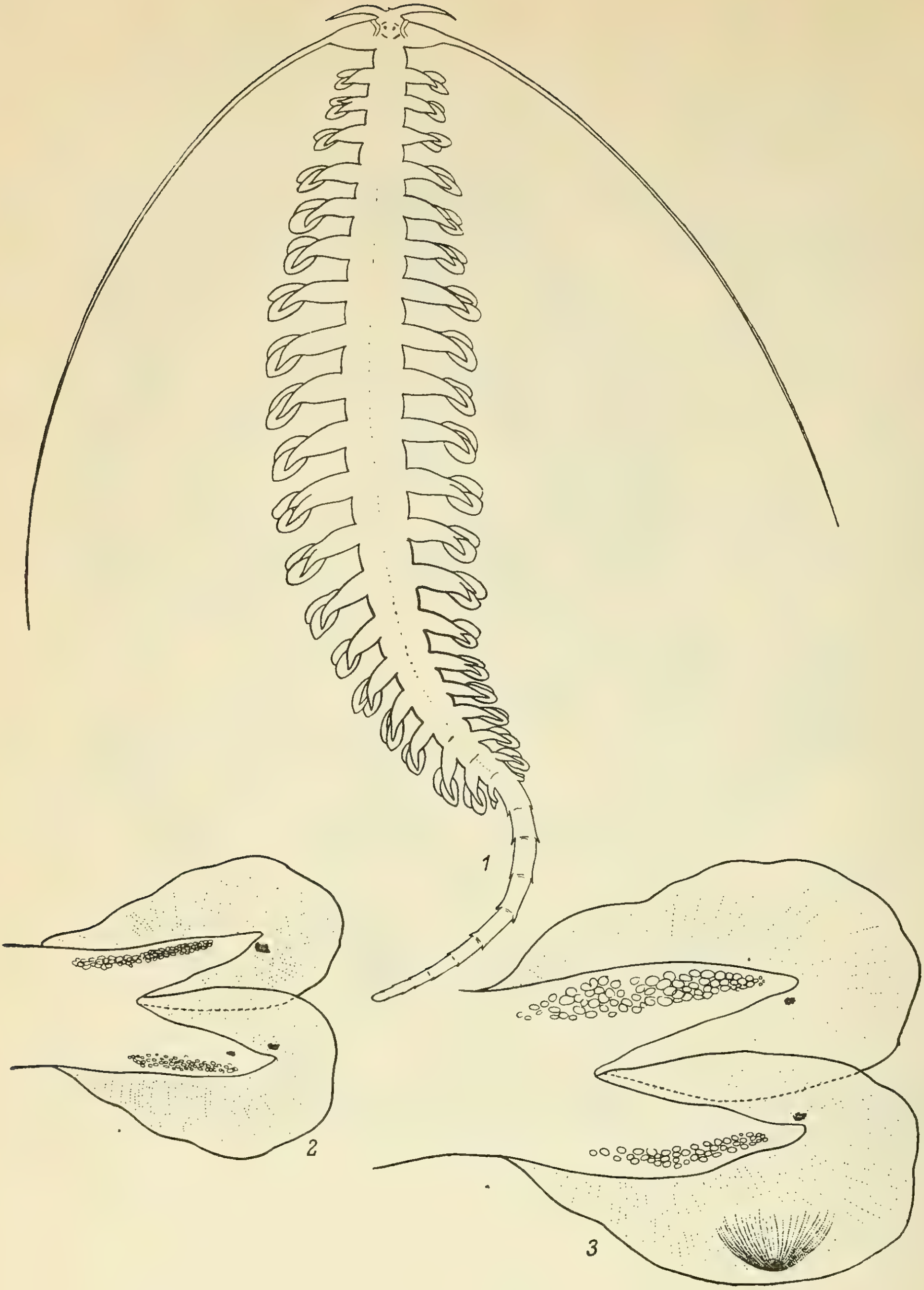

PLATE XXXI

Tomopteris (Johnstonella) helgolandica Greeff: 1) general view, dorsal; 2) 1st parapodium; 3) parapodium from middle of body (North Atlantic).

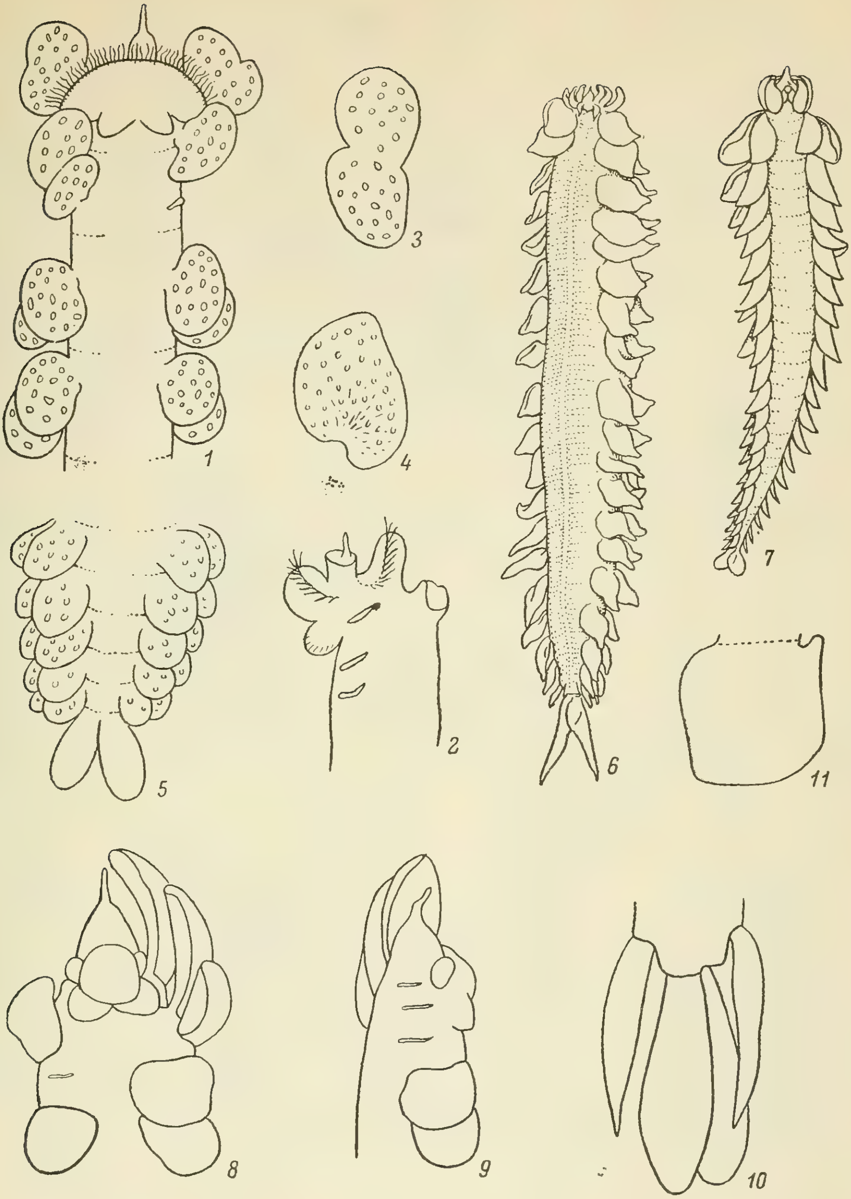

PLATE XXXII

Typhloscolex muelleri Busch: cephalic end, dorsal; 2) same, lateral (cirri lost); 3) tentacular cirri; 4) podial cirrus from middle of body; 5) posterior end (Northwest Pacific).
Travisiopsis lanceolata Southern: 6) general view, dorsal (after Wesenberg-Lund, 1939).
Travisiopsis lobifera Levinsen: 7) general view, dorsal (after Tebble, 1962).
Travisiopsis levinseni Southern: 8) cephalic end, dorsal (cirri on left side lost); 9) cephalic end, lateral; 10) posterior end; 11) podial cirri from middle of body (Northwest Pacific).

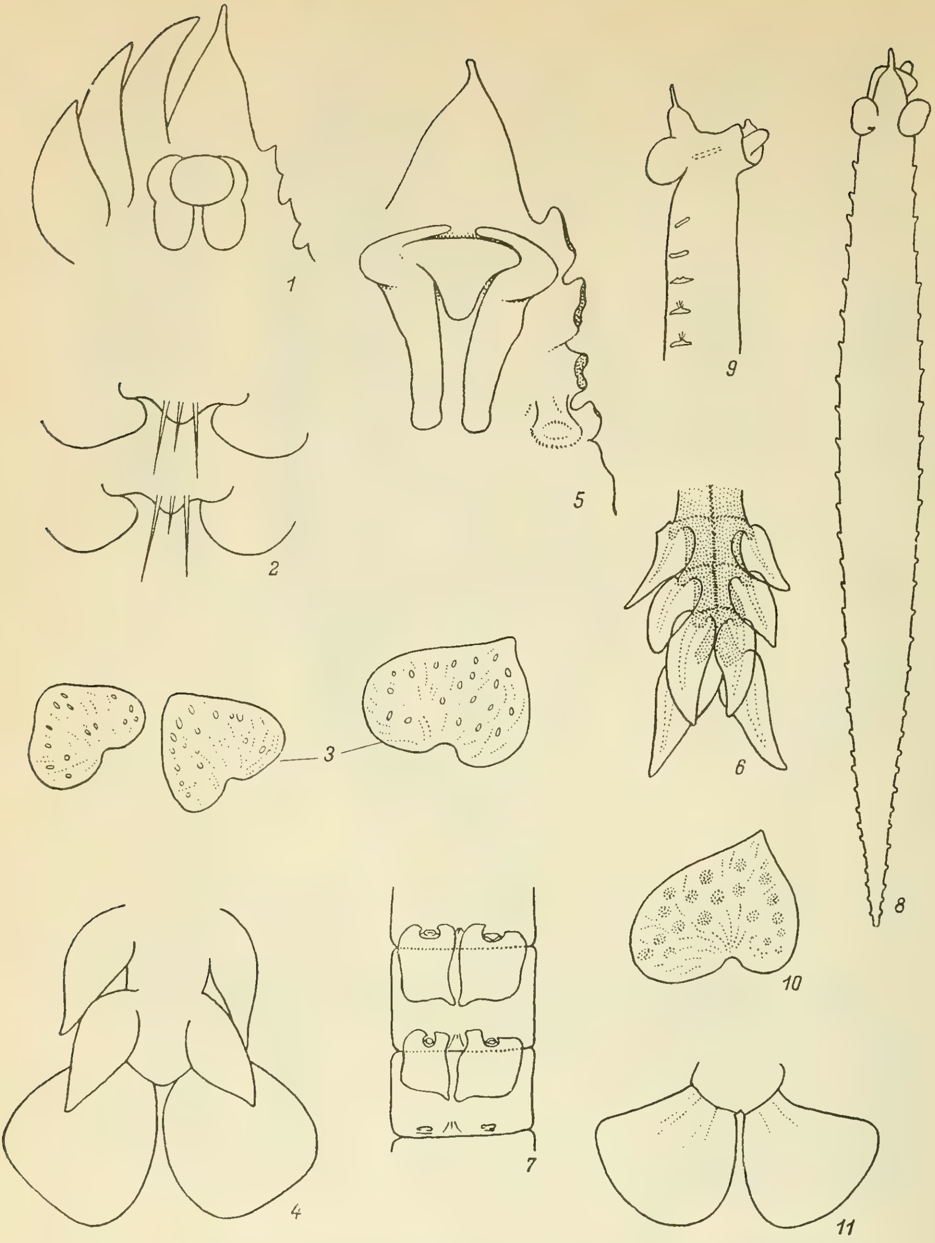

PLATE XXXIII

Travisiopsis lobifera Levinsen: 1) cephalic end, dorsal (cirri of right side lost); 2) podial lobes with setae; 3) podial cirri; 4) posterior end (Northwest Pacific).

Travisiopsis lanceolata Southern: 5) cephalic end, dorsal (cirri lost); 6) posterior end; 7) body segments, lateral (after Southern, 1911).

Sagitella kowalewskii Wagner: 8) general view, dorsal (all cirri lost); 9) cephalic end, lateral (cirri lost); 10) podial cirrus; 11) anal cirri (Northwest Pacific).

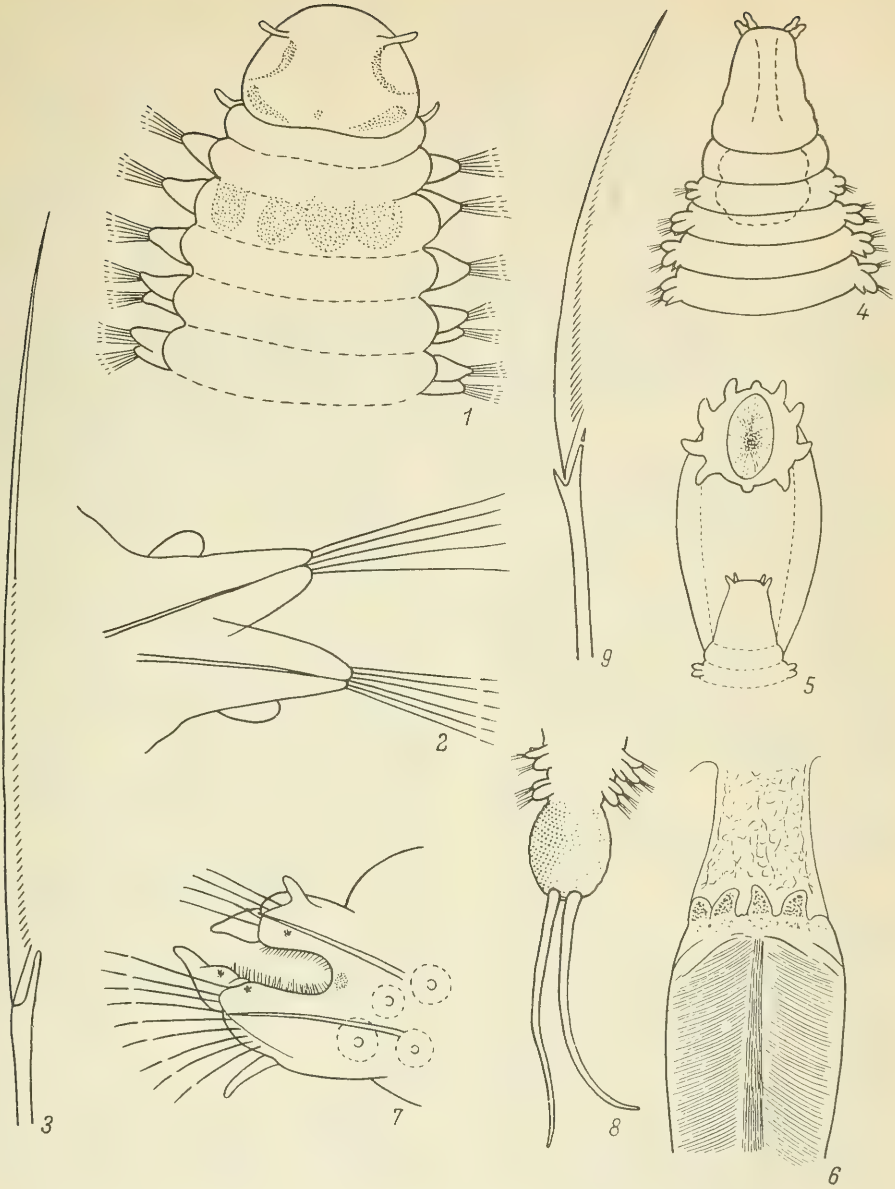

PLATE XXXIV

Lacydonia papillata Uschakov: 1) cephalic end, dorsal; 2) parapodium from middle of body; 3) seta (Kuril-Kamchatka Trench, type).
Paralacydonia paradoxa Fauvel: 4) cephalic end, dorsal; 5) everted pharynx; 6) sagittal section of pharynx; 7) parapodium from middle of body; 8) posterior end; 9) ventral seta (Yellow Sea).

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* [Reproduced photographically from the Russian original. Page numbers refer to those of the Russian, which appear in the left-hand margin of this translation.] Taxonomic units above the genus shown in bold face, synonyms in italics. Bold face numerals denote pages on which a description is given; an asterisk refers to pages of the Introduction in which figures or maps are given; Roman numerals denote numbers of Plates.

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